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The Breeding Seasons of East African Birds

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Acknowledgements

It will be clear to all readers that a major paper of this nature, published by an entirely voluntary organisation, can only be made possible by a great deal of hard and devoted work by a large number of people. The contribution made by the authors is perhaps obvious, but on behalf of the Society and myself, I would like to pay tribute to a number of 'behind the scenes' workers.

Without the meticulous records kept by our very able Nest Record Scheme Organiser, Mrs Hazel Britton, the work would not have got off the ground; but even she would have been quite helpless without the numerous observers who sent in their cards in such numbers and with such regularity.

Equally important has been the contribution made by our Hon. Editor, Mrs Jean Hayes, who has had the somewhat thankless and unglamourous task of putting the manuscript through all its stages of editing and printing; a herculean effort. But I know that she, in her turn, would wish to acknowledge the help willingly given by members of the Society's Ornithological and Editorial sub-committees.

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So our sincere thanks go to the authors, to those who made donations, and all other members, too numerous to mention, for making possible a publication which the Society considers to be a major contribution to ornithological literature. Nowhere in East Africa or elsewhere in the tropics has so detailed an attempt been made to compile such a mass of information, and to relate it to climatic factors in an effort to assess the true reasons for breeding at a particular time of the year.

It is, therefore, with a feeling of pride that we present this work, to commemorate fittingly the 70th Anniversary of our Society this year.

July 1979

John Karmali Chairman

E.A. Natural History Society

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Introduction

The last major discussion of the breeding seasons of East African birds and their possible relationships with climatic factors and food supply was that of Moreau (1950). At that time, comparatively little was known of the breeding seasons of East African birds; and the nesting of some abundant species (for instance, the Lesser and Greater Flamingos Phoeniconaias minor and Phoenicopterus ruber) was unknown. Accordingly, Moreau's tentative conclusions, valuable as they were, were often based on inadequate evidence. Moreover, the climatic factors, which are the proximate cause of vegetative growth (and, through this, the abundance or scarcity of certain foods) were inadequately understood. Since then, the climatic variations characteristic of East Africa have been better studied and a large body of new data on the breeding dates of many species has accumulated. A new analysis of the situation has therefore seemed overdue.

The breeding seasons of birds in countries to the north and south of East Africa have been summarised by Archer & Godman (1961), for Somalia; by Benson et al. (1971), for Zambia; and by Urban & Brown (1971), for Ethiopia (admittedly imperfectly understood). Within East Africa, a study of the breeding seasons of birds in the Arusha National Park by Beesley (1973) summarises 1276 records (some of them duplicated on East Africa Natural History Society nest record cards) and discusses these in relation to climateand food supply. It is the most valuable local study available. This area, however, forms part of region D, one of our five much larger geographical areas based on climate, and may not be entirely typical of it.

This paper attempts to bring together all that is known, to date, of the breeding seasons of East African birds, and to relate these, so far as possible, to the climatic factors (especially rainfall) controlling scarcity or abundance and seasonal changes of various foods. We have attempted not only to gather together unpublished records from many sources, but to include all *accurate dated* records published in literature applying to East Africa. Many records in the existing literature are not accurately dated, and their original source cannot always be located.

This study includes a total of 86 331 dated records (excluding five species, the Great White Pelican Pelecanus onocrotalus, two species of flamingos, the Sooty Tern Sterna fuscata, and the Red-billed Quelea Quelea quelea, which together run into millions) for 861 of the 1123 species accepted as East African residents. We feel that it is an advance on anything hitherto attempted for East Africa and should serve as a base-line for future research on this subject. Perusal will show, however, that for a great many species, some very common and wide-spread (e.g. the White-crowned Shrike Eurocephalus anguitimens), our knowledge of breeding seasons, and consequently of the factors affecting them is still very incomplete.

Table 1 summarises the data available by categories of numbers. From this it will be seen that for 439 out of 861 species for which any records at all exist we have ten or fewer records. Of these we have only indicative records for 54 species and dated records for 385. For another 114 species we have 11-20 records, and for only 308 species are there more than 20 dated records. One hundred and fifty four species, many of them colonial, have more than 50 dated records. We are perfectly aware that, for a statistical analysis, a minimum sample of 20 is considered barely adequate. However, if we had accepted any such limitations, this paper could not have included available data for 545 species. While less than 20 records for any species in one or more climatic regions may be inadequate for statistical analysis they can still be clearly indicative of breeding peaks, for instance the Peregrine Falcon Falco peregrinus. Still smaller figures, of less than five records, for many species of small passerines frequently support the available records for a few well documented species, for example, among larks, pipits and many warblers.

Thus, although we feel that this paper is an advance on anything hitherto published and permits sound (or, at least, reasonable) conclusions to be drawn for many species, it remains inadequate for many others. We hope that the publication of this material—imperfect as it obviously is—will act, firstly, as an encouragement for the many people who have sent in records and, secondly, as a spur to ornithologists or other naturalists (especially those living and working in areas now inadequately covered) to provide records of even common species which might normally be thought too trivial to be of any importance.

The systematic order and nomenclature of this paper have been based on that of White (1960-1965) as the only available checklist of African birds south of the Sahara. At family level, we have followed A. L. Thomson (1964) in the nonpasserine families; but, in the order Passeriformes, we have followed the arrangement of Benson et al. (1971)—itself based upon Wetmore (1960) but recognising some additional families. We are aware that this arrangement is not likely to be followed in the forthcoming revision of the Peters' Checklist of the Birds of the World (D. W. Snow, in litt.), but we have adhered to it because several other African checklists follow this order (Benson et al. 1971; Benson & Benson 1977) and because this order will be used for the forthcoming East African list of bird species, to be published by the East Africa Natural History Society during 1980. By this means, we hope to avoid confusion with other East and Central African lists, even though the order of passerine families adopted is not likely to be standard in future.

The order of non-passerine families adopted by Benson et al. (1971), and in this paper, does not differ from that of other lists. White's order and nomenclature has been revised in the light of recent work on several families by several authors—for example, Kahl (1971) for Ciconiiformes; Brown & Amadon (1969) for Falconiformes; and Fry (1969)

for Meropidae. With a few minor exceptions, the nomenclature conforms with that in the forthcoming East African list of birds. We have not attempted to relate the nomenclature of White or Benson to that of Mackworth-Praed& Grant (1957,1960)—the standard reference work on East African birds-since the systematic order in this book is very different from that of others quoted. However, for ease of crossreference by readers, our species headings identify each species listed including Mackworth-Praed & Grant's serial number thus: Sterna repressa Whitecheeked Tern M-P&G 353. If no number is shown, this indicates that the species is not listed in Mackworth-Praed & Grant and may be a West African or other species, only recently recorded in East Africa. Readers should therefore find it easier to relate the data in this paper both to the main available reference work and to White's checklists.

This paper covers Kenya, Tanzania and Uganda. Central and southern Tanzania is very much more poorly covered, in relation to its total area, than any other of five main geographical regions based on climatic variations within these three countries. However, breeding seasons in southern Tanzania may be expected to conform more closely to those of other parts of the *Brachystegia* woodland belt, well documented for Zambia by Benson *et al.* (1971), than to Kenya or even northern Tanzania.

Kenya is the most ecologically and climatically complicated of the three countries, including within her boundaries the whole of one of our climatic regions and segments of four others. Uganda, the smallest, and Tanzania, the largest of the three countries, each contains only two not the same. Thus, the opportunities for assessing the local effects of climate upon food supply and breeding seasons are better in Kenya than elsewhere; but such effects may be more clear-cut and easier to analyse, where records are sufficient, in Tanzania or Uganda. Normally, there are more records for eastern Kenya, northern Tanzania, and parts of Uganda (especially near Entebbe and the Kabalega National Park) than for other regions in almost any species.

Definition of Breeding Season

The breeding season of any bird includes five phases, more or less clearly distinct from one another:

(a) song and display (b) nest-building or repair (c) the incubation period (d) the fledging period (e) the post-fledging period when young are out of the nest but still dependent on their parents. The duration of these combined phases may be from one month (in the smallest passerines) to over twenty-two months (in the Crowned Eagle Stephanoaetus coronatus). In many large species, it apparently precludes breeding more than once a year; but, in some small passerines—for example, the African Pied Wagtail Motacilla aguimp—it permits the production of a succession of broods (up to eight attempts in 13 months).

Following most recent authors, who have based their approach on that of Moreau (1950), we consider that a definite attempt to breed has not been made until an egg has been laid. We have accordingly calculated the onset of the breeding season in all cases to the egg-laying date, which is sometimes difficult in large species with protracted fledging periods. In a few cases, where other good data are lacking, we have included oviduct cggs as indicative of breeding seasons. Display, song, and nest-building may not necessarily be followed by egg-laying, or a definite attempt to breed. In most such cases, however, we have one or more definite egg-dates to reinforce these prelimininary—and more easily observed—phases of the whole breeding season.

Sources of Data

Material has been gathered from the following sources:

(a) The East African Nest Record Card Scheme, initiated in 1969 and contributed to by ornithologists from all over East Africa. This is an extension of an East Africa Natural History Society scheme, initiated in 1961 at the instigation of L.H.B., to obtain breeding records from National Parks and other similar sources and for some years organised by the late M. E. W. North. In 1965, he handed over the collected material to L.H.B. but it still appeared too fragmentary for a worthwhile analysis. Accordingly, the EANHS record card scheme was started in the hope of obtaining fuller coverage; it is still only partially realised. This scheme has been (and is) organised by Hazel A. Britton, to whom we make grateful acknowledgement for an immense

amount of hard detailed work.

Response to this scheme has been extremely poor from some sources. For instance, despite repeated appeals, not a single record has been received from the Serengeti Research Institute, from the Uganda Institute of Ecology (formerly the Nuffield Unit for Tropical Animal Ecology), the Tsavo Research Institute, or from the Nakuru Wildlife Trust (formerly the Baharini Wildlife Sanctuary).

It will be apparent to our critics who complain that the material given herein is insufficient for statistical analysis that, had such organisations (or individuals resident for long periods in the same locality) provided much more detailed data, more thorough analysis related to many factors would have been possible. We suggest, therefore, that such institutes should early establish a collection of record cards, not only for birds but for other species. In time, such accumulated records can be of incalculable value, especially in relation to local conditions. A standard EANHS nest record card takes about two minutes to prepare in the field when the nest is first found; it is permanent, can be photocopied as often as need be and can be added to on subsequent visits until no further records are made at the nest. Preparation of such permanent data is not an onerous task.

Many other ornithologists and observers of wildlife have mentioned interesting records to us which they do not trouble to record on cards, even when given to them. While the availability of such records would, to some extent, improve the completeness of our data, we feel that records which are neither published nor recorded on cards are best discarded. Nevertheless, we have augmented—in some cases greatly—what is available on cards by personal data and records collected from individuals who have studied particular subjects, but who have not filled in cards in all cases. For instance L.H.B. has here included many raptor records not on cards (though much of his material is now entered on cards).

Individual scientists attached to National Parks and research institutes, however, have independently sent us many valuable records. Notable among these have been J. S. S. Beesley, P. C. Lack, W. Leuthold, S. Mungure and C. Smeenk. Indeed, most record cards have been sent in by individual

ornithologists. Besides our own, we should mention Miss D. Angwin, G. C. and Mrs D.E. G. Backhurst, Miss E. J. Blencowe, G. R. Cunningham van Someren, A. D. Forbes-Watson, W. G. Harvey, Dr and Mrs G. C. Irvine, J. S. Karmali, J. H. E. Leakey, C. F. Mann, B. S. Meadows, J. F. Reynolds, Miss S. Sassoon, the late P. H. B. Sessions, N. J. Skinner and Mr and Mrs J. Start.

Some eggs which were in the National Museum, Nairobi, are no longer to be found there, though a dated record still exists. Several individual scientists who have worked in National Parks on ornithological or other subjects have been approached and have given us records, which have now been extracted onto cards by us. These include Dr A. R. E. Sinclair (about 250 records from Serengeti); Dr D. C. Houston, whose records of vultures in Serengeti exceed all those of vultures elsewhere; L. Hurxthal who has studied ostriches for several years in Nairobi National Park; J. B. D. Hopcraft, for water birds on Lakes Nakuru and Naivasha; and D. A. Turner, who not only provided a large number of his own cards (now duplicated by us) but many other records from his notebooks. Results from such long-term or specific studies have often been specially useful and we thank the scientists who have helped us with such records.

Finally, Mrs H. A. Britton has been privileged to extract onto cards a great deal of valuable unpublished information from the egg-registers of the late Captain C. R. S. Pitman, whose records have been specially useful in regard to Uganda (Regions A and B). Without them, we should have comparatively few accurate, dated records from these areas. Captain Pitman's records normally give precise data on clutch size, egg-dates, state of incubation, measurements etc., so that it has sometimes been possible (in individual cases) to calculate precise laying dates. Mrs Britton has also extracted onto cards the data available from the collection of the National Museum, Nairobi; the Belcher collection in that museum; some of the collections of the Paris and Durban museums; and of Dr V. G. L. van Someren. In some cases, especially among passerines, these records have added significantly to the bulk of material available for many species. G. R. Cunningham van Someren has recently made available to us material from the original record books of V.G.L. and R.A.L.

van Someren, dating back to 1906.

Some cards have been discarded as being too vague to establish definitely the laying dates of the species concerned. This applies especially to species such as large raptors, storks, or pelicans, with a long breeding cycle, and nesting perhaps in inaccessible tall trees where the contents of the nests cannot easily be ascertained. In such species, the egg-laying date may differ by several months from that of the observation. However, with insight and from experience, we have tried to interpret as many such cards as possible, even though, in a few cases, this may lead to some small errors in establishing the laying date.

We wish to point out that one good, accurately-dated card—with full details of nest site, size, height above ground, and contents seen—is more valuable than several indefinite cards. This applies especially to common species for which a large number of records may already be available and where indefinite data are now largely unnecessary. Those species which are common, but whose nesting dates are little known, and those rare species for which almost any sort of indicative data would be valuable will be readily identified from this paper. We thus hope to help later workers to discriminate where an indicative if vague record would be useful and where it would not.

Some species of Palaearctic distribution, such as the Osprey Pandion haliaetus and the Common Sandpiper Actitis hypoleucos have not been recorded as breeding in East Africa in recent years, despite very much larger numbers of keen observers, though there are a few old records, sometimes doubtful and the subject of controversy. There are also a few cases on record cards where the identification of a species may be in doubt or where, (for instance one June record of Wahlberg's Eagle Aquila wahlbergi), the laying date is so much at variance with all other records that it could be erroneous in an easily-confused species. We believe that all such doubtful records, whether on cards or from any other source, are best not admitted, though we have sometimes indicated their source.

For every species where the data are sufficiently comprehensive (usually with more than 50 single records or more than 500 colonial records) we have prepared a summary card, on which all available

data, including that from the literature, up to end June 1976 have been recorded. The summarised data include laying dates; clutch and brood sizes recorded; incubation periods and fledging periods, etc. These summary cards are retained by the EANHS record scheme and filed with the other cards for the species. While we appreciate that our interpretation of available results may be questioned, anyone interested in a particular species can re-examine the cards and other data and make his own interpretation. Cards utilised by us have been marked with a small red spot; and in some cases where we have calculated the laying date from available data we have entered these details on the card concerned. As other species attain the necessary level of numbers of records they can be similarly summarised.

(b) The available literature: we have studied not only the standard reference books available for East Africa (some of which repeat information that is available on individual cards or in shorter papers) but also as many individual papers referring to East Africa as we have been able to locate. At an early stage of this study, a bibliography prepared by P. L. and H. A. Britton was circulated to some 30 people or institutions, with a request for any desirable additions. From the small number of replies received (in fact, only six), we have assumed that few titles had been omitted and any listed, or later published, are now incorporated. The literature consulted has also been listed on a reference card for every species, with definite dated records extracted in red ink. These literature cards are filed with the species records.

Undoubtedly, we may have missed a few interesting records in this way, but often the material available from the literature is only a fraction of that available from cards (with a few notable exceptions, such as storks, flamingos, pelicans, or East African Lari, where recent full review papers have summarised available data). In some cases, records on cards may duplicate those in the literature, but we have tried to allow for this possibility. Data in the literature are often, also, repeated from book to book; or they repeat data which we have otherwise recovered and listed on cards. In some cases, the data from the literature are too imprecise to enable accurate analysis by geographical region and, sometimes, a place named has been hard to find. Also, in the literature, most

records of—for instance—colonies of water birds are of a very general nature and give few (or no) precise egg dates, inadequate details of variation in clutch-size, and so on. Any doubtful cases in the literature have been discarded although, when they concern rare species, they may be mentioned. In the summarised records for each species which follow, we have combined all definite dated literature records with those from cards and other sources. For a few species, there are more records in the literature than on cards; for example, the African Dwarf Bittern *Ixobrychus sturmii*.

We believe that, by these various methods, we have extracted as much accurate information as is practicable up to the end of June 1976. In a few species—for example, the Black-headed Heron, Ardea melanocephala—we have included later data when these made a substantial difference to the knowledge available (in this case, the only dated breeding records for the coastal region).

If there are individuals or organisations with unpublished information whose data have not been made available to us, it is not for want of trying on our part.

In the analysis of the available data, L.H.B. has been responsible for the non-passerines and P.L.B. for the passerines. The introductory and discussion sections have been jointly discussed and compiled.

Sources of Bias

We have divided the species into categories according to the completeness of the data available to us. However, even when the data may appear sufficiently comprehensive to permit a reasonable analysis according to climatic regions, they may still be subject to bias. Evidently, the most useful records are those gathered by keen observers, often in the field, who reside in one area for a long period of time, or who are engaged upon specific surveys. Thus, for birds of prey detailed surveys in Embu district, on several lakes, and in the Tsavo National Park (Brown 1952, 1955, 1960, 1966, 1972; Smeenk 1975) have been especially valuable. Even here, however, the data for the African Fish Eagle Haliaeetus vocifer are biased to some extent by the large sample (nearly half the total) from Lake Naivasha, where 56 pairs were recorded for two years. One keen observer working in a certain area over part of a year may still produce more records from that area than all the rest together, and so bias the results. However, such cases are few.

Equally, individual observers may, by their own methods, introduce bias. J. S. S. Beesley, in his last months as warden in the Arusha National Park, concentrated upon finding nests, and thus obtained more records than would normally have been obtained in such a short period. The late Dr. V. G. L. van Someren, at Karen, concentrated on finding nests principally in the long rains, April and May, so that his data are biased in favour of that period.

The data from the nest record card scheme, randomly collected by many observers all over East Africa are less likely to be subject to such individual bias. However, more observers are likely to be in the field in the dry season than in the height of the rains, whentravel may be difficult and unpleasant, especially in remote areas, though in fact most breeding may occur in the rains, especially among passerines.

Where it appears to us that such sources of bias have had a marked effect on the results, as summarised, we have mentioned it in discussion under the species concerned. In small samples of less than 20 records altogether (applying) to a large number of species), we consider that such sources of bias are normally unimportant. However, we mention these factors to show that, as far as possible, we have taken sources of bias into account in our specific analyses.

Climatic Regions

East Africa, lying astride the Equator, and with very high mountains creating, in many cases, their own local variations of climate, is far more difficult to study climatologically than, for instance, West Tropical Africa which is mainly lowland and, where the rainfall decreases in regular succession from coastal areas to the Sahara desert, with consequently regular vegetation belts running approximately parallel to the coast (Cochemé 1967, Cochemé & Brown 1970).

Moreau(1950) and other authors have pointed out that the single most noticeable climatic effect in tropical regions is the alternation between dry and wet seasons. In our area, therefore, we have based our five major eco-climatic regimes principally on rainfall; and on the classification of East African rainfall regimes proposed by Griffiths (1958), which has also been used by several other recent authors—for example, Pratt & Gwynne (1977), in relation to vegetation types. However, we have simplified Griffiths' ten regions into five larger groupings, each with basically similar rainfall characters, and with relatively minor variations in pattern, though not in amount (Map 1). To analyse our records in relation to ten different regions—some varying from one another only in degree—would often have resulted in too few records from any one region to indicate any clear relationships between breeding seasons and the main climatic criterion of seasonal rainfall.

We are aware that some of our regions, notably Region D, are far too large and ecologically complex to be ideal. We have been criticised for not taking into account much more local variations than would even be evident had we used all ten of Griffiths' regions. Such criticisms can only be countered by collecting much more detailed records; evidently this would be most valuable in, for instance, research stations dealing with smaller parts of one of our large regions, where the accumulated records could later be compared with other records—for example, of rainfall in different years. In the absence of such more precise local data we have tried to discuss available breeding data in relation to principal rainfall regimes.

In temperate climates, the effect of low winter temperatures is overriding. Increasing warmth in spring, with increasing day length and development of green vegetation, is the main factor initiating breeding seasons. In Equatorial latitudes, the effect of temperature is related to altitude rather than season. The mean annual temperature falls by about 1°C per 300 m of altitude, this effect varying only slightly in the East African highlands. A drop in temperature is often associated with an actual increase in rainfall, or at least an increase in available soil moisture through reduced evaporation. This results in an often bewildering sequence of vegetative zones from the bottom to the top of even quite a small mountain or range. Moreover, on such very high mountains as Kilimanjaro and Mt Kenya, very cold 'winter conditions' occur nightly, and relatively warm 'summer conditions' daily. Apart from a few species confined to these regions—such as the Scarlettufted Malachite Sunbird Nectarinia johnstoni—we have too few dated records to make a discussion of breeding dates related to these temperature variations worthwhile. Where we have any such records they have been discussed under the individual species concerned. Sometimes, montane members of a species breed at a different time to others of the same species—for example, the Augur Buzzard Buteo rufofuscus.

In broad terms, in any region, the higher the total annual rainfall the more reliable it is, and the longer the period over which it falls. Thus, in Region A, rainfall of over 1000 mm/vr in the Gulu district of Uganda is more reliable and long-sustained than rainfall of less than 500 mm in semi arid Karamoja, only about 150 km northwards. In Region D, typified by two alternating dry and wet seasons annually—with the long and short rains separated by dry seasons of varying intensity and severity-total rainfall varies from over 1600 mm/yr to under 200 mm/vr. At the lower figure, one or both rains may fail completely, and any breeding must then be purely opportunistic. Rainfall histograms illustrating differences in such patterns are given in Fig. 1. Some bird species vary greatly in their ecological tolerance. They may start to breed in some areas in, for example, March, but not till May in a drier area. Where sufficient records are available this generally shows up as a peak; but a species may have been recorded in only one part of a large range, and this can lead to bias. Where such bias appears we have tried to indicate it in the species accounts.

It is sometimes hard to ascribe a record to a particular region, as it may be from a point near the boundary where the rainfall pattern is not quite typical of the region as a whole. This is particularly difficult in some parts of Kenya. However, most records fall clearly into one region or another; and where there is any doubt, we have tried to resolve it as best we can in the light of available information. For instance, a record from Mau Narok district in Kenya is in Region A, while records from lower Narok and the Mara Game Reserve are in Region C. Evidently, some records 'from Narok District' could come from either.

Our five main simplified climatic regions (Map 1) are as follows:

Region A: northern tropical single-season rainfall regime, with one main rainy season in the wetter parts March-October and in the drier parts May-September, in each case with a period of lower rainfall about June-July (Griffiths' zone 2). This pattern extends over most of northern Uganda about as far south as the Kabalega (Murchison) Falls National Park, and southward along the Rift Valley to Baringo and Kericho in Kenya. Records from Mau Summit, Mau Narok, Kabarnet, West Nandi, Eldoret, Kitale, Kapenguria, Lessos and Timboroa have been included in this region.

Rainfall histograms typical of ten selected stations in Region A varying from 645–1981 mm mean annual rainfall, averaging 1285 mm show that only small parts of this region are relatively arid, and that one good rainy season can be expected every year. About 60% of the total rainfall occurs between April and August on average, and the three driest months are December, January and February, each with less than 4% of annual rainfall, totalling 8.83%. The main dry season, though hot, is not quite so dry as in Region C.

Region B: western Kenya, Lake Victoria Basin, and Uganda, with a main rainy season March-November, but with two sub-peaks April-May and October-November; a drier period June-September but always with some rain in these months. The main dry season is November-March. This includes Griffiths' sub-zones 5 and 6, with a curious lobe-like process running north-east of Lake Kyoga. This region includes Entebbe, Kampala, Rwenzori National Park, Bwamba, Kisumu, Kakamega and Kaimosi. It is the second best-known of our regions, largely through the efforts of C. R. S. Pitman, V. G. L. van Someren, F. J. Jackson, and others. It includes the main lowland forest areas of western Kenya and Uganda and, accordingly, most bird species of basically West African distribution.

Rainfall histograms for ten selected stations in Region B varying from 764-1956 mm/yr, averaging 1453 mm, show that none of this region is very dry, and that although the rainfall is decidedly bimodal in pattern, the peaks are much less abrupt than in Region D. 37% of annual rainfall occurs between March and May, and there is then a much drier break in June-July with rainfall again increasing

with another 26% of annual rainfall between September and November. Only one month, January, has less than 5% of the annual mean.

Region C: the Southern Tropical single-season rainfall regime. This includes Griffiths' zone 7 and his small zone 4 (south Narok District), typified by a single main rainy season, (the opposite of that in Region A), with rain between October and April or May, with local variations according to amount, but normally 750 mm or over annually. The rainy season is followed by a protracted-often hot and sunny-dry season, May-October. Lake Victoria is approximately bisected by the boundary between this and Region B. The boundary thereafter runs south-east to meet the coast south of Dar es Salaam. Localities on or near the border of this region include Bukoba in Tanzania and Narok in Kenya. This very large region includes most of Tanzania and, in relation to its size, is farless documented than any other of our regions. As mentioned, however, breeding seasons in this region are more likely to resemble those of Zambia or Malawi than those of Kenya or even northern Tanzania.

Rainfall histograms for 12 selected stations typical of Region C, varying from 566-1149 mm/yr and averaging 886 mm show that 77% of annual rainfall occurs from December to April, and that June to October each have less than 3 % of the annual total, 9.37% of the annual total falling in these five months. Although this long dry season is more intense than that in Region A, it is relatively cool as the sun is then over the northern tropic and much of the interior of Tanzania is a plateau more than 1000 m A.S.L. This results in what Moreau called 'the cool dry season', whereas the similar long dry season in Region A is often much hotter. In this region, the pattern for Narok, close to the border of Region D, is somewhat atypical, but has been included because many records come from 'Narok District'.

Region D. Equatorial, east of the eastern Rift, two-season rainfall regime. This area runs in a vast arc from northern Turkana east of the Uganda escarpment through the summits of Mt Kenya and the Aberdares including northern Tanzania in the Kilimanjaro region—and, meeting the coast south of

Dar es Salaam, includes Griffiths' sub-zones 1, 8 and 9. It borders on Region A in the north, and on Region C in the south, coming very close to Region B in western Kenya. It includes Kilimanjaro, the Usambaras, Manyara, Olduvai, Ngorongoro, Tanga, Dar es Salaam, Zanzibar, Pemba, Mafia, Morogoro and Kilosa in Tanzania. It is characterised by two rainy seasons-the long rains March-May and the short rains late October-December. In high rainfall areas, these may be prolonged from March-June and October-end December; but, in lower rainfall areas, they occur April-mid May and November-mid December. The rainy seasons are separated by dry seasons of different character, that from June-October being relatively cool and mainly overcast, that from January-March much hotter and mainly sunny.

We have used the word 'cool' in the relative sense, following Moreau (1950), Lack (1954) and other authors. Above 1800 m A.S.L., the June-October dry season is genuinely cool, even cold, with minimum temperatures below 8°C at Nairobi. At Magadi, at 613 m A.S.L., mean monthly minimum temperatures never fall below 21°.8C and the climate can never be described as 'cool'.

The rainfall is highly variable, erratic in pattern, and unreliable. There is no such thing as a normal year in much of this region. Moreover, it may vary locally in a confusing manner. For instance, on the northern slopes of Mt Kenya in Meru district, the short rains October-December are more reliable; but on the southern slopes the April-May rains are more important. On the western slopes, near Nanyuki (in Griffiths' small sub-zone 3) much rain falls July-August when the eastern slopes are dry and overcast, or, at higher altitudes, misty. Since many species occur all over the areas concerned, their breeding patterns may be highly confusing. However, this is to some extent overcome by the relatively much larger number of records from this region than from any other, largely because of the greater number of keen observers who have lived or worked in one part of Region D or another.

Rainfall histograms for 20 selected stations in Region D demonstrate the variability of rainfall both in amount and pattern. The variation in mean annual rainfall is from 178 mm in desert at Lodwar to 1926 mm in tropical forest at Amani, averaging

overall 1022 mm. Overall, 46% of rainfall occurs in the long rains March-May and 30.58% in the short rains, October-December. However at Meru 38% of the annual rainfall occurs March-May and 48% of the total from October-December, so that here the "short" rains are the heavier. This is also true of Isiolo and Voi, both semi-arid localities where the short rains are somewhat greater in amount than the long rains. Morogoro is rather atypical of Region D, resembling more the pattern of Region C, and clearly transitional.

Region E: the Kenya coast (Griffiths' zone 10) receives most rain from April-June, during the southeast monsoon (but very erratic and variable) with some rain falling at other times of the year and sometimes protracted into July, August and November, but decreasing rapidly with distance inland from the coast itself towards Region D. It is open to question whether records from this region should be combined with those of Region D; but, since it is of special importance for colonial seabirds and species of lowland coastal forests, we have preferred to keep it as a separate region. Thus far, results appear to justify this step; in fact, coastal records from Region D near Dar es Salaam might be more appropriately included in Region E, though at present the data are inadequate to show this clearly.

Rainfall histograms for six stations from north to south of Region E all but one, (Kwale, in the Shimba Hills) on the coast, show that over half the year's rain can be expected in April-June (53.69%) while 25.23% falls in one month, May. Only in January and February does less than 2% of the annual rainfall occur. This varies somewhat from place to place, but the pattern is distinctive, with one major peak and some rain in most months, justifying the retention of this small Region as a separate entity.

It is often difficult to ascribe a particular record correctly to one or other of these particular regions, owing to minor rainfall variations. Thus, most of the Serengeti ecosystem is included in Region C;

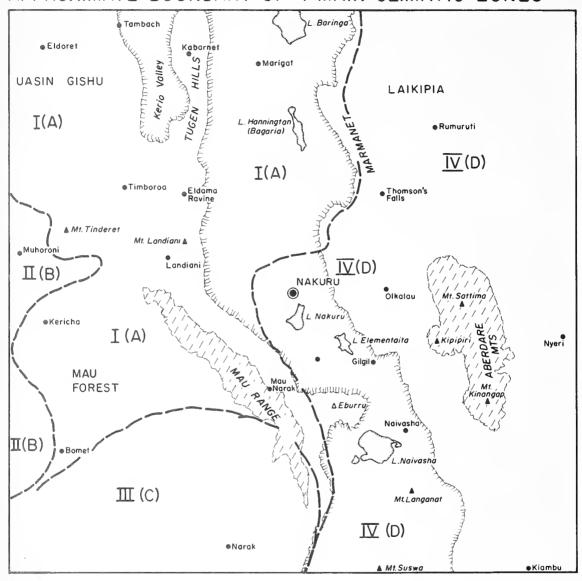
but there are large annual variations of rainfall within this area which control the movements of vast herds of migratory ungulates (vide e.g. Vesey-Fitzgerald 1974, and Norton-Gritfihs et al. 1975). The breeding patterns of birds in the Serengeti, from which we have few really accurate records, is likely to be affected by these local variations. Likewise, west of Nanyuki to Maralal, in Region D, there is a small area with regular rain July-August, sothat such species as the Long-tailed Widowbird Euplectes progne and Jackson's Widowbird E. jacksoni may come into breeding condition and nest at a different time of year to that at Naro Moru, less than 40 km away. The rainfall pattern of the Mau Narok plateau in Kenya at 3000 m A.S.L. west of the Rift is basically that of Region A; while at Nakuru, only about 50 km away, on the floor of the Rift at 2000 m, it is clearly that of Region D. Lake Baringo, on the floor of the Rift, but at 1500 m, is in Region A, while Lake Nakuru 60 km south is in Region D.

The extreme complication of local rainfall variations and total amount is exemplified by the variations included in a 100 km circle based on the town of Nakuru, which includes segments, as shown on Map 2, of four of our regions; varies in amount from less than 500 mm to over 2000 mm; and in altitude from over 4000 m to 1000 m. Species with short breeding cycles, such as many passerines, require a large number of records precisely dated and accurately located to clarify the relationship between rainfall, food supply, and breeding seasons. Species with longer breeding cycles, such as many large birds of prey, may show a less close relationship; and may be obliged to breed at a time of year which is not ideal for all their requirements, whereas in a region with a clearer alternation of wet and dry seasons they may show a definite peak at one or other season. However, at this stage it would be unprofitable to attempt a more detailed analysis of these relatively enormous variations within a small area. We do, however, think it desirable to draw attention to this area and the contribution a detailed study of it could make to the solution of relations between breeding seasons, rainfall, vegetative growth, and abundance of various foods.



MAPI: MAIN CLIMATIC ZONES OF EAST AFRICA (Griffiths 1958)

MAP II. 100 KM. SQUARE CENTRED ON NAKURU, SHOWING APPROXIMATE BOUNDARY OF 4 MAIN CLIMATIC ZONES





▲ Mountain..... Mt. Longonat

Mountain range over 2,700m.

WILLIAM Rift Valley Escarpment

 $\overline{I(\Delta)}$ Approximate boundary of Climatic Zane

T(A) Narthern Trapical Regime

III(C) Sauthern Trapical Regime

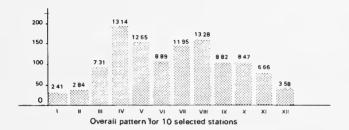
IV (D) East Of Rift Bimodal Regime

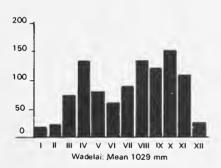
RAINFALL PATTERNS in the five main climatic regions outlined in Map. 1. (Source: Kenya Meteorological Department).

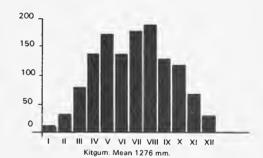
NOTES: (1) All rainfall measurements are in mm

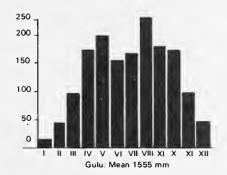
(2) In histograms showing overall pattern for each region, figures at the tops of columns give the percentage of annual rainfall occurring each month.

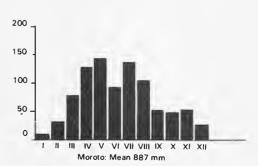
Region A

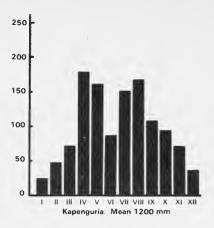


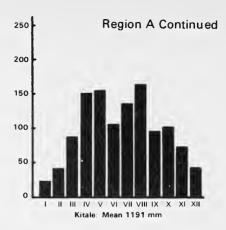


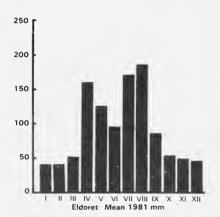


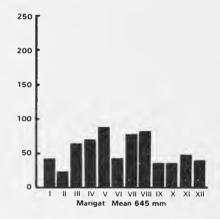


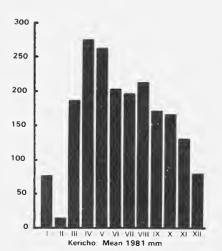


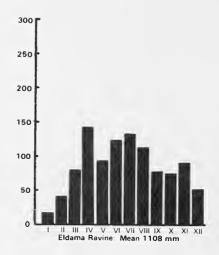


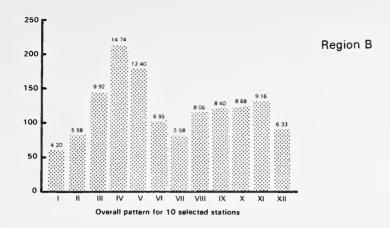


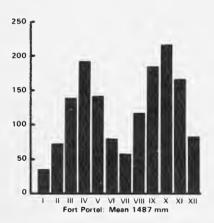


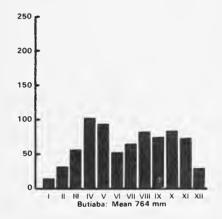


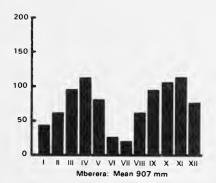


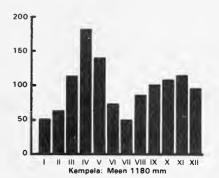


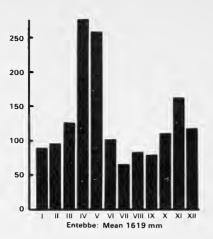


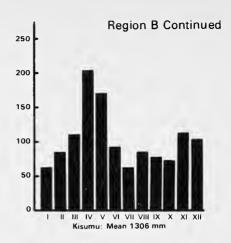


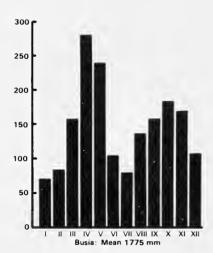


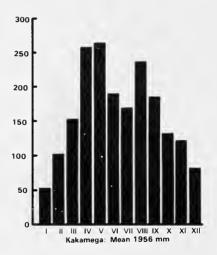


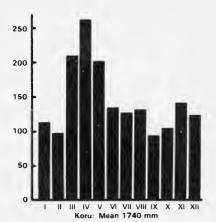


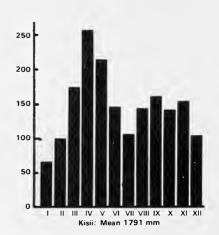




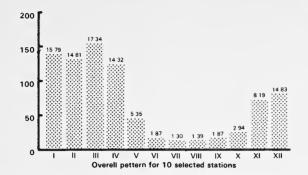


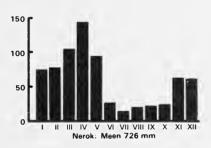


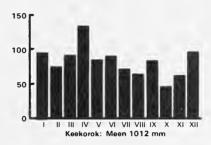


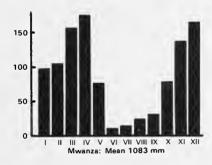


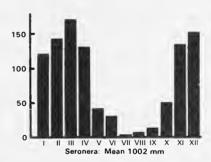
Region C

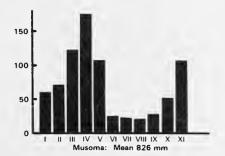


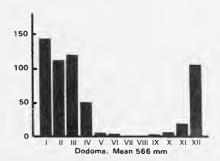




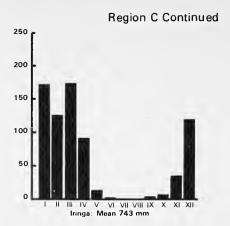


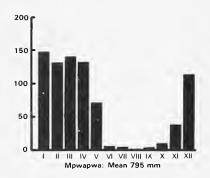


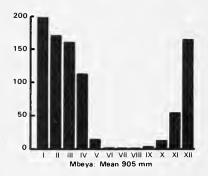


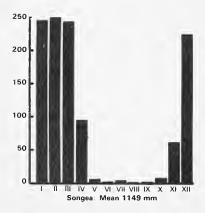


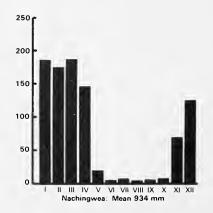
1 II III IV V VI VII VIII IX X XI XII Tabora. Mean 894 mm

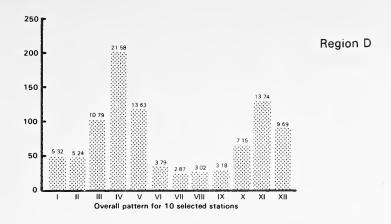


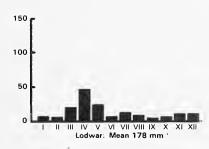


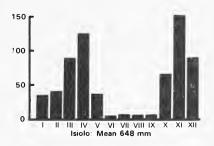


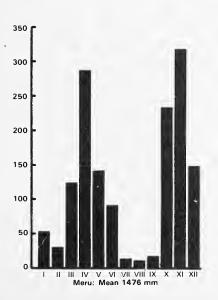


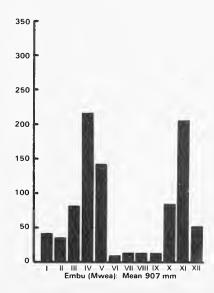




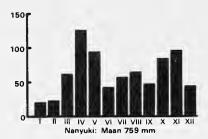


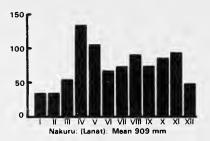


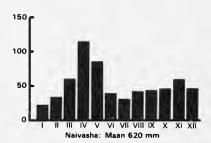


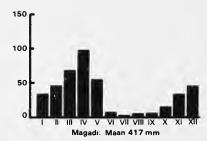


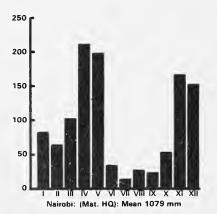
Region D Continued

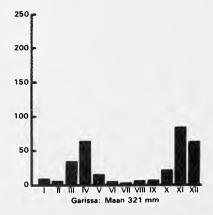




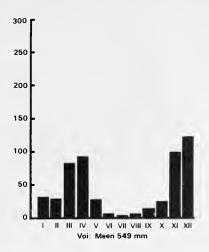


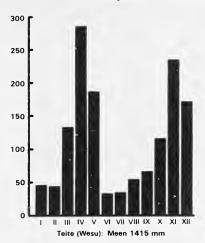


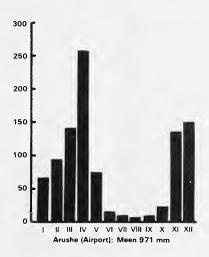


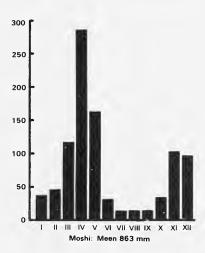


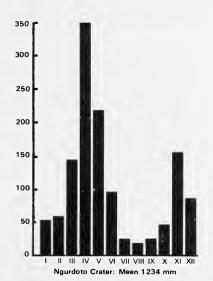
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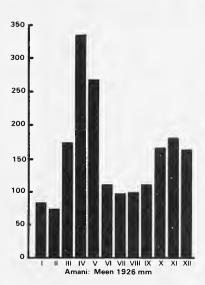




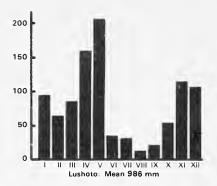


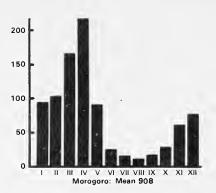


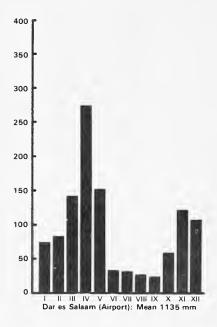


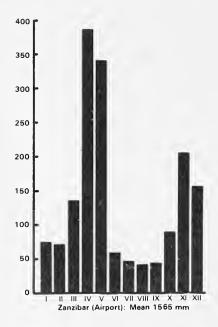


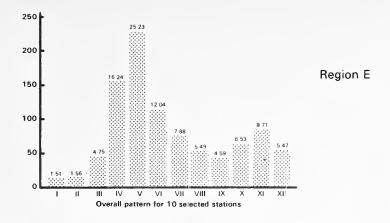
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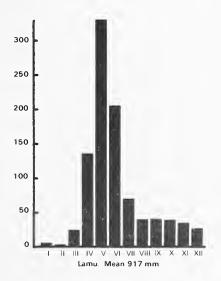


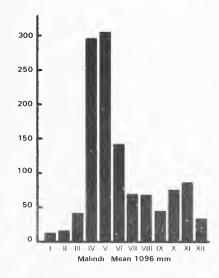


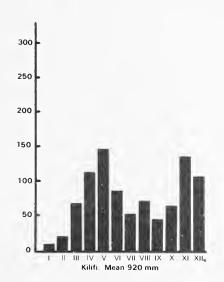


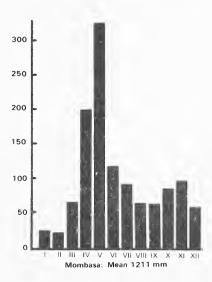


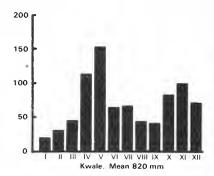


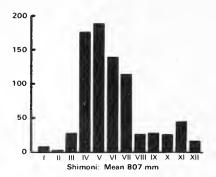














Categories of Species by numbers of records

The East African list, according to White (1960-1965), together with our variations, includes 1105 breeding (or presumed breeding) species, some of which are intra-African migrants. For our purposes, we have divided these into 10 categories, according to the number of records available, as detailed below.

In the record section, it will be seen that categories (1) and (2) have been listed separately. These are followed by categories (3)–(10), which have been placed in systematic order. Brief details are given for the records in categories (3)–(6); but the last four categories (7)–(10), with more than 20 dated records, merit more detailed discussion. The category number and the number of cards used are indicated in the species heading, thus:

Tachybaptus ruficollis Little Grebe M-P&G 4 Category (8) 79 records.

We have also used symbols, in certain cases, to indicate status, such as abundance, endemicism and so on.

We felt that this method of analysis might help later workers to distinguish between those species for which a considerable bulk of data exists and those little-known but common species for which a large amount of new data could be gathered relatively simply by a directed effort.

The categories of species by number of records are:

- (1) III species whose nests, so far as we know, remain undescribed (for instance, the Northern Brownbul *Phyllastrephus strepitans*, a common species of north Kenya coast gardens);
- (2) 150 species whose nests have been found outside East Africa but for which no definite dated East African records exist. Many of these are extralimital, just reaching East Africa at, for instance, Bwamba and are uncommon or rare. Some may not even be resident, though the possibility that they breed in our area should not be overlooked. Examples are the Taita Falcon Falco fasciinucha and Anchieta's Sunbird Anthreptes anchietae;
- (3) 54 species for which a few indicative records exist, but for which we have no precise egg dates; for instance, the Swallow-tailed Kite *Chelictinia riocourii* and the Slender-billed Greenbul *Andropadus gracilirostris*;

- (4) 269 species with 1-5 definite dated records, too few for analysis, but indicative when related to others of their family. Examples are the White-backed Night Heron Nycticorax leuconotus, with three records, all from the literature, suggesting laying either in the rains or dry season, and the White-throated Greenbul Phyllastrephus albigularis with four records, Region B, all March-April in the long rains;
- (5) 116 species with 6-10 dated records. If most of these are in one region, and closely grouped, they can be indicative of a breeding peak. For example, the Senegal Thicknee, Burhinus senegalensis, has 8 records, all in Region A, indicating a breeding peak in the dry season, and the Rock-loving Cisticola Cisticola aberrans has 6 records, from Region C, January-March, middle-end rains. Evidently many species now in this category could soon be lifted into Category (6), (7) or higher;
- (6) 114 species with 11-20 definite records, often with more than 10 in one region, useful for analysis. An example is the Rufous Short-toed Lark *Calandrella rufescens* with 12 records, seven in May, indicating a breeding peak in the main rains;
- (7) 154 species with 21-50 definite records, usually with 10 or more in more than one region, and therefore useful for more detailed analysis in relation to climate. An example is the Pale Flycatcher *Bradornis pallidus*, with 27 records in all regions, mainly in region D, suggesting a widespread breeding season, in both rains in regions B and D, prolonged in region E from April-September, peaking in June;
- (8) 77 species with 51-100 definite records, usually suitable for analysis in relation to climate for more than one region. An example is the Black-winged Plover *Vanellus melanopterus*, with 63 records—12 in Region A and 47 in Region D—clearly suggesting breeding peaks in both regions;
- (9) 51 species with 101-500 records, capable of good analysis in relation to climate in several regions. For each such species, fuller details have been given, followed by a more thorough discussion of the factors involved. An example is the African Fish Eagle *Haliaeetus vocifer*, with 275 records—36 in Region A, 108 in Region B, and 122 in Region D—which can be further subdivided into separate river or lake systems;

(10) 26 species with more than 500 records. Most of these are colonial species, such as the larger herons, storks and ibis; or ploceid weaver birds. Examples are the Great White Pelican Pelecanus onocrotalus and the Black-headed Weaver Ploceus cucullatus. Despite the fact that these samples are large or very large (involving even millions of pairs in the Lesser Flamingo Phoeniconaias minor and Red-billed Quelea Quelea quelea) they may sometimes be more subject to bias than those in category (9), which more often consist of a large number of single records.

When a waterbird colony is visited, few observers make accurate counts of nests, of those containing eggs or young, or of clutch and brood size. Sometimes this is due to lack of time, or to avoid excessive disturbance; but some of the early records of this type (Jackson (1938) on the Kisumu Heronry, for instance, and some of the records from the Belcher and Pitman collections) refer to single (or a few chosen) clutches taken from a much larger colony whose total numbers were not even approximately recorded and which might have contained 50–1000, or more, pairs at different stages. With colonial weavers, the most agile man is often unable to reach more than a small sample of nests overhanging deep water or pendant from the tips of high branches.

Future workers are advised that, where possible, accurate counts of nests, clutch sizes, brood sizes and other such details are more valuable than a mere general statement of numbers breeding.

Within each of these categorics, records from

cards, literature, and any other sources have been combined to produce (as far as possible) a comprehensive picture of present knowledge. For most of the better-known species, cards have provided the bulk of the data. In the main, species with large numbers of records are discussed more thoroughly than are others; in some cases, however, the conclusion is so clear that it needs little discussion. For instance, Wahlberg's Eagle Aquila wahlbergi, breeds August-November, peaking September-October, throughout its East African range, irrespective of the climatic conditions. On the other hand, the Ostrich Struthio camelus appears to lay in the dry season all over East Africa; but this behaviour cannot always be clearly correlated with food supplies for young or adults and a longer discussion of the factors involved is therefore necded.

Grouping of Species by type of food or habitat

Bird species can also be divided into categorics according to the type of food they eat, habitat, nest site, and so on—for example, ground-nesters, treenesters or hole-nesters.

We have felt that a fuller analysis of such factors is best placed in a discussion section at the end of this paper. Here, we endeavour only to relate the available knowledge to previously-expressed views (which may be erroneous) or to special features concerned with survival, which may affect some species.

Table 1. Records analysed by families and numerical categories

Note:

(a) Categories I & 2, (breeding unknown, or no East African records) excluded.
 (b) Species with more than 50 000 records (Pelecanus onocrotalus, Phoenicopterus ruber, Phoeniconoias minor, Sterna fuscata and Quelea quelea) not totalled, shown by asterisk in family.

This column excludes families which occur in East Africa but do not breed, e.g. Procellariidae, Fregatidae.	Species with breeding records	(3) Indicative only	(4) 1–5 records	(5) 6-10 records	(6) 11–20 records	(7) 21–50 records	(8) 51–100 records	(9) IOI-500 records	(10) Over 500 records	Total records
		<u> </u>		<u> </u>				<u> </u>	Ü	<u> </u>
A. NON-PASSERINE FAM										
Struthionidae	I							I		106
Podicipitidae Pelecanidae	3 2				I		2	I	1*	168 27 6+
Sulidae	2 I							1	I	500-550
Phalacrocoracidac	2								2	2308+
Anhingidae	Ī								I	899
Ardeidae	16		4			I	2	4	5	19 801
Balaenicipitidae	I	I	•					•	-	51
Scopidae	I					I				23
Ciconiidae	6		I		2			I	2	5793
Threskiornithidac Phoenicopteridae	5 2	I					I	I	2 2*	7511
Anatidae	14			_	2	5		I	2	425
Accipitridae	40	2	9	5 7	3 4	10	5	3		1462
Sagittariidae	I	-	9	/	4	I	ر	3		45
Falconidae	IO	I	5	2	I	I				74
Phasianidae	19	I	3	5	I	8	I			359 88
Numididae	4		I		2		I			
Turnicidae	3	I		I	I		_			29
Gruidae	I	_	_	_			1			99
Rallidac Heliornithidae	15 1	5	3 I	3	I	I	2			258 2
Otididae	6		2	I	2	I				69
Jacanidac	2		ī	•	-	•	I			72
Rostratulidae	Ī		_	I						9
Charadriidae	13			2	I	3	2	5		928
Scolopacidae	I(?2)		31			I				21 (?22
Recurvirostridae	2					I	I			117
Burhinidae	3			I		I	I			126
Glareolidae	7			I	3	I 2	2	2	4+1*	245 24 291
Laridae Rhynchopidae	IO I	I				2	I	2	471	79 79
Pteroclidae	5		2			3	1			79 89
Columbidae	17	I	3		3	4	5	I		662
Psittacidac	9	2	5		2	•	-			49
Musophagidae	13	2	5 5 3	2	3	I				96
Cuculidae	15	3	3	2	2	4	I			222
Tytonidae	2		1			I				31
Strigidae	10	2	3	2	2	3				114
Caprimulgidae	13 12	4	4	5	3 I	I I	I	2		115 650
Apodidae Coliidae	3	4	3 1		1	1	I	I		279
Trogonidae	2	I	-		I		_	_		13
Alccdinidae	13		3	5	I	3	1			208
Meropidae	12	I	5	_	1	_	3		2	272 3
Coraciidae	5	2	I		I	1				42
Upupidae	I					I				22
Phoeniculidac	_5	_	2	2	I	_				42
Bucerotidae	12	I	4	2	4	1	I			112
Capitonidae	23	Ι	12 1	2 2	4 2	3	1			231 41
Indicatoridae Picidae	5 11		6	3	I	I				78
Ficiuae	11		Ü	5	•	•				, 0
Total 52 Non-Passerine Fami	lies 383	33	95	56	52	66	36	23	23	72 003

MILY	Species with breeding records	(3) Indicative only	(4) I-5 records	(5) 6-10 records	(6) 11-20 records	(7) 21–50 records	(8) 51–100 records	(9) 101–500 records	(10) Over 500 records	Total records
PASSERINE FAMILIES										
Eurylaimidae	2		2							4
Pittidae	2		2							3
Alaudidae	16		8	3	2	2	I			176
Hirundinidae	14		2		3	5	2	2		590
Dicruridae	2		I			I				49
Oriolidae	4		3			I				34
Corvidae	7	I	2	I	I	I	1			113
Paridae	6		4	I		I				36
Remizidae	I			I						9
Certhiidae (Salpornithidae)	I		I							2
Timaliidae	II		7		2	2				107
Campephagidae	3		I	I	I					21
Pycnonotidae	21	2	8	2	4	4		1		611
Turdidae	37	I	16	5	4	5	5	I		826
Sylviidae	70	2	31	7	12	12	4	2		1290
Muscicapidae	32	2	13	4	3	6	3	I		625
Motacillidae	16		5	3	3	2	I	2		426
Malaconotidae	2 I		ΙΙ	3	3	2	2			289
Laniidae	8		3	I	1	I	I	I		381
Prionopidae	5		2	I	2					39
Sturnidae	24		9	6	2	6	I			330
Nectariniidae	41	3	13	5	2	12	3	3		1131
Zosteropidae	3					3				117
Ploceidae Ploceinae	53	4	9	6	5	7	8	ΙI	2+1*	5080
Bubalornithinae	3		I		I	I				52
Passerinae	13	I	2	3	I	2	2	2		621
Viduinae	7		2	I	2	2				55
Estrildidae	39	4	11	6	8	5	4	I		790
Fringillidae	15	I	5			5	3	I		520
Total 26 Passerine Families	477	21	174	60	62	88	41	28	3	14328
Total All species	861	54	269	116	114	154	77	51	26	86 331

Breeding records grouped by categories (according to number of species concerned)

Categories (1) and (2) are listed without additional comments, except where specified. In these lists, the following symbols are used:

- X nest and eggs undescribed but site known
- * East African endemic
- † locally common, or abundant, whose nests should not be difficult to find
- ø may not be resident

For certain of these species, the nest and eggs remain unreported; in some cases, however, we have acceptable breeding data which indicate the breeding season. In such cases, we have listed the species twice—once here and again later, in systematic order.

Category (1) Species whose nests were undescribed up to June 1976

(a) Non-passerines 44 species

Dryotriorchis spectabilis Congo Serpent Eagle M-P&G

Accipiter castanilius Chestnut-flanked Goshawk

Urotriorchis macrourus Long-tailed Hawk M-P&G 181

- † Francolinus nobilis Handsome Francolin M-P&G 205 Sarothrura lugens Chestnut-headed Crake M-P&G 234 Sarothrura affinis Chestnut-tailed Crake M-P&G 230 Himantornis haematopus Nkulenga Rail
 - Columba albinucha White-naped Pigeon M-P&G 381 Agapornis lilianae Lilian's Lovebird (eggs desc.) M-P&G 453
 - Agapornis swinderniana Black-collared Lovebird M-P&G 456
- X Pachycoccyx audeberti Thick-billed Cuckoo (hosts known) M-P&G 412
- † Cercococcyx mechowi Dusky Long-tailed Cuckoo M-P&G
 409
- X Cercococcyx olivinus Olive Long-tailed Cuckoo M-P&G
 410
- X Cercococcyx montanus Barred Long-tailed Cuckoo M-P&G 411
 - Chryscoccyx flavigularis Yellow-throated Green Cuckoo M-P&G 419
- * Otus ireneae Sokoke Scops Owl
 Otus rutilus Pemba Scops Owl M-P&G 535
 Glaucidium teplironotum Red-chested Owlet M-P&G 539
 Glaucidium castaneum Chestnut Owlet

Caprinulgus stellatus Star-spotted Nightjar M-P&G 555 Apus berliozi Forbes-Watson's Swift Schoutedenapus myoptilus Scarce Swift M-P&G 639 Neafrapus cassini Cassin's Spinetail

Apaloderma vittatum Bar-tailed Trogon M-P&G 571 † Halcyon senegaloides Mangrove Kingfisher M-P&G 474

(see discussion)

Phoeniculus castaneiceps Forest Wood Hoopoe M-P&G

524

- X Tockus camurus Red-billed Dwarf Hornbill (sites known, eggs undesc.) M-P&G 514
- X Tockus hartlaubi Black Dwarf Hornbill M-P&G 513
- X Lybius rolleti Black-breasted Barbet (sites known, eggs undesc.) M-P&G 572

Lybius minor Black-backed Barbet M-P&G 577
Lybius rubrifacies Red-faced Barbet M-P&G 579
Pogoniulus coryphaeus Western Green Tinkerbird
M-P&G 593

Pogoniulus simplex Green Tinkerbird M-P&G 591 Indicator conirostris Thick-billed Honeyguide (hosts known) M-P&G 609

Indicator exilis Least Honeyguide (some hosts suspected) M-P&G 610

Indicator meliphitus Pallid Honeyguide M-P&G 610 Indicator narokensis Kilimanjaro Honeyguide M-P&G 611

Indicator pumilio Chapin's Least Honeyguide Melignomon zenkeri Zenker's Honeyguide

Prodotiscus zambeziae Eastern Honeybird M-P&G 613 Prodotiscus regulus Wahlberg's Honeybird (some hosts suspected) M-P&G 612

Dendropicos gabonensis Gabon Woodpecker

- X Mesopicos xantholophus Yellow-crested Woodpecker M-P&G 632
- X Mesopicos elliotii Elliot's Woodpecker M-P&G 633

It is of interest that, in the above list, a high proportion of non-Passerines is composed of nest parasites (five cuckoos and eight honeyguides) and of hole-nesting barbets, woodpeckers or hornbills, in which sites may be known but eggs or young remain undescribed.

(b) Passerines 67 species

Pseudocalyptomena graueri Grauer's Broadbill

- † Mirafra hypermetra Red-winged Bush Lark M-P&G 657 Mirafra pulpa Friedmann's Bush Lark M-P&G 654
- * Mirafra williamsi Williams' Bush Lark M-P&G 660 A
 Oriolus nigripennis Black-winged Oriole (sites known)
 M-P&G 1169

Trichastoma poiiothorax Grey-chested Illadopsis M-P&G

Kakamega albipectus Scaly-breasted Illadopsis M-P&G 737

Phyllanthus atripennis Capuchin Babbler M-P&G 739 A Campephaga petiti Petit's Cuckoo-Shrike M-P&G 1082 Andropadus gracilis Little Grey Greenbul M-P&G 772 Andropadus ansorgei Ansorge's Greenbul M-P&G 772 A Baeopogon clamans Sjostedt's Honeyguide Greenbul

† Chlorocichla laetissima Joyful Greenbul M-P&G 770 Thescelocichla leucopleura White-tailed Greenbul M-P&G 748

† Phyllastrephus strepitans Northern Brownbul M-P&G
754

Phyllastrephus baumanni Toro Olive Greenbul M-P&G 760

Phyllastrephus lorcuzi Sassi's Olive Greenbul Bleda eximia Green-tailed Bristle-bill M-P&G 747 Nicator vireo Yellow-throated Nicator M-P&G 1149

† Cerconela scotocerca Brown-tailed Rock-chat M-P&G 870

Atethe poliophrys Red-throated Alethe M-P&G 904
* Dryocichloides montains Usambara Ground Robin
M-P&G 906

Dryocichloides archeri Archer's Ground Robin M-P&G 886

* Dryocichloides lowei Iringa Ground Robin M-P&G 907

† Sheppardia aequatorialis Equatorial Akalat M-P&G 898 Cossypha roberti White-bellied Robin Chat Modulatrix orostruthus Dappled Mountain Robin M-P&G 762

X Neocossyphus poensis White-tailed Ant Thrush M-P&G
849

Turdus camaronensis Black-eared Ground Thrush Turdus princei Grey Ground Thrush Turdus tanganjikae Kivu Ground Thrush Turdus oberlanderi Forest Ground Thrush Bradypterus graueri Grauer's Warbler M-P&G 949

† Bradypterus carpalis White-winged Warbler M-P&G 950 Bradypterus alfredi Bamboo Warbler M-P&G 951 Chloropeta gracilirostris Papyrus Yellow Warbler M-P&G 958

* Cisticola restricta Tana Cisticola

Apalis nigriceps Black-capped Apalis M-P&G 983

* Apalis karamojae Karamoja Apalis M-P&G 988
Apalis argentea Kungwe Apalis M-P&G 990
Apalis moreaui Long-billed Apalis M-P&G 989
Bathmocercus winifredae Mrs Moreau's Warbler M-P&G
992

Drymocichla incaua Red-winged Grey Warblet M-P&G

Fremomela turneri Turner's Eremomela M-P&G 1007
Hemitesia neumanni Short-tailed Warbler
Macrosphenus concolor Grey Longbill M-P&G 1015
Macrosphenus flavicans Yellow Longbill 1014
Batis perkeo Pygmy Puff-back Flycatcher M-P&G 819

X Erythrocercus mccallii Chestnut-capped Flycatcher M-P&G 808

† Erythrocercus holochlorus Little Yellow Flycatcher M-P&G 807

* Authus sokokensis Sokoke Pipit M-P&G 710
Laniarius mufumbiri Papyrus Gonolek M-P&G 1120
Laniarius fuelleborni Mountain Sooty Boubou M-P&G
1124

* Malaconoms alius Uluguru Bush Shrike M-P&G 1145

Prionops caniceps Red-billed Shrike M-P&G 1094
Nectarinia oustaleti Angola White-bellied Sunbird
M-P&G 1250

Nectainia bouvieri Orange-tufted Sunbird M-P&G 1247

* Nectarinia moreaui Moreau's Sunbird M-P&G 1255

* Ploceus golandi Clarke's Weaver M-P&G 1320
Ploceus albinucha Maxwell's Black Weaver (nesting suspected) M-P&G 1354

Ploceus olivaceiceps Olive-headed Golden Weaver M-P&G 1338, 1340

Malimbus erythrogaster Red-bellied Malimbe M-P&G 1357

Parmoptila jamesoni Red-fronted Ant-pecker

Clytospiza cinereovinacea Dusky Twinspot M-P&G 1415 Cryptospiza shelleyi Shelley's Crimson-wing M-P&G 1401

Nigrita luteifrons Pale-fronted Negro Finch (site known) M-P&G 1387 A

Spermophaga poliogenys Grant's Bluebill M-P&G 1392

In the above list, a large proportion is extra-limital with main distribution in West Africa, just entering East Africa; a high proportion represents skulking forest species of greenbuls, akalats, etc. The Northern Brownbul Phyllastrephus strepitans appears to be almost unique in its abundance in East Africa; but details remain unknown.

Category (2) Resident (or presumed resident) and breeding species whose nests are known elsewhere but for which there are no definite East African breeding records:

(a) Non-passerines 58 species

† Sula leucogaster Brown Booby M-P&G 19
Circaetus cinerascens Banded Snake Eagle M-P&G 157
Accipiter erythropus Red-thighed Sparrowhawk M-P&G
171

Buteo auguralis Red-necked Buzzard M-P&G 168
 Spizaetus (Cassinaetus) africanus Cassin's Hawk-eagle
 M-P&G 148

Falco fasciinucha Taita Falcon M-P&G 114
Francolinus lathami Forest Francolin M-P&G 189
Francolinus clappertoni Clapperton's Francolin M-P&G
202

Turnix hottentota Black-rumped Button Quail M-P&G 366

Ortyxclos meiffi enii Quail Plover M-P&G 367
Canirallus oculcus Grey-throated Rail M-P&G 220
Porzana pusilla Baillon's Crake M-P&G 228
Porzana marginalis Striped Crake M-P&G 226
Sarothi ura boehmi Böhm's Crake M-P&G 231
Sarothrura elegans Buff-spotted Crake M-P&G 236
Sarothrura pulchra White-spotted Crake M-P&G 235
Otis ai abs Arabian Bustard M-P&G 249

† Neotis hcuglinii Heuglin's Bustard M-P&G 252

 Vanellus supercitiosus Brown-chested Wattled Plover M-P&G 288

- Ø Dromas ardeola Crab Plover M-P&G 335 Pluvianus aegyptius Egyptian Plover M-P&G 334
- Ø Sterna albifrons Little Tern M-P&G 357
- Ø Sterna bengalensis Lesser Crested Tern M-P&G 355 Columba unicincta Afep Pigeon M-P&G 382 Columba malherbii Western Bronze-naped Pigeon Streptopelia reichenowi White-winged Dove M-P&G 389
- † Turtur abyssinicus Black-billed Wood Dove M-P&G 396 Cuculus gularis African Cuckoo M-P&G 404 (d) Centropus cupreicaudus Coppery-tailed Coucal Bubo poensis Fraser's Eagle Owl M-P&G 545 Scotopelia peli Pel's Fishing Owl M-P&G 546 Glaucidium capense Barred Owlet M-P&G 540 Asio otus Long-eared Owl M-P&G 530
- † Caprinulgus nubicus Nubian Nightjar M-P&G 553
 Apus barbatus Black Swift M-P&G 636
 Chaetura sabini Sabine's Spinetail M-P&G 649
 Telecanthura ussheri Mottled-throated Spinetail M-P&G
 647

Urocolius indicus Red-faced Mousebird M-P&G 569 Halcyon malimbica Blue-breasted Kingfisher M-P&G 475

Halcyon badius Chocolate-backed Kingfisher M-P&G 478

Coracias spatulata Racquet-tailed Roller M-P&G 459 Phoeniculus granti Violet Wood Hoopoe (if a good species) M-P&G 520

Phoeniculus aterrimus Black Wood Hoopoe M-P&G 523
Tockus hemprichii Hemprich's Hornbill M-P&G 512
Tockus pallidirostris Pale-billed Hornbill M-P&G 511
Tropicranus albocristatus White-crested Hornbill
M-P&G 502

Ceratogymna atrata Black-wattled Hornbill M-P&G

Bycanistes fistulator Laughing Hornbill M-P&G 498 Bycanistes bucinator Trumpeter Hornbill M-P&G 497 Bycanistes cylindricus White-thighed Hornbill M-P&G 499

Buccanodon whytii Whyte's Barbet M-P&G 587 Pogoniulus atroflavus Red-rumped Tinkerbird Sasia africana African Piculet

Campethera bennettii Bennett's Woodpecker M-P&G 618 Campethera cailliautii Little Spotted Woodpecker M-P&G 620

Campethera nivosa Buff-spotted Woodpecker M-P&G

Dendropicos stierlingi Stierling's Woodpecker M-P&G 628

(b) Passerines 92 species

Mirafra collaris Collared Lark M-P&G 663

- † Eremopterix nigriceps White-fronted Sparrow Lark M-P&G 680
- † Eremopterix signata Chestnut-headed Sparrow Lark M-P&G 681

- Galerida modesta Sun Lark M-P&G 677
- Ø Hirundo albigularis White-throated Swallow M-P&G 1056
- Ø Hirundo dimidiata Pearl-breasted Swallow M-P&G 1058
- Ø Hirundo cucullata Larger Striped Swallow M-P&G 1065 A
- O† Oriolus auratus African Golden Oriole M-P&G 1165
 Parus afer Grey Tit M-P&G 1151
 Parus griseiventris Miombo Grey Tit M-P&G 1151
 Remiz musculus Mouse-coloured Penduline Tit M-P&G
- † Alcippe abyssinica African Hill Babbler M-P&G 740 Turdoides leucopygius White-rumped Babbler M-P&G 728

Turdoides aylmeri Scaly Chatterer M-P&G 733

† Coracina pectoralis White-breasted Cuckoo Shrike M-P&G 1085

Ixonotus guttatus Spotted Greenbul M-P&G 752 Chlorocichla simplex Simple Greenbul

Phyllastrephus scandens Leaf-love M-P&G 750

Phyllastrephus cabanisi Cabanis' Greenbul M-P&G 758 Phyllastrephus cerviniventris Grey-olive Greenbul M-P&G 759

Phyllastrephus xavieri Xavier's Greenbul M-P&G 763 Phyllastrephus icterinus Icterine Greenbul

Oenanthe bottae Red-breasted Wheatear M-P&G 866 Pentholaea albifrons White-fronted Black Chat M-P&G 874

Monticola angolensis Mottled Rock Thrush M-P&G 852 Cercotrichas barbata Bearded Scrub Robin M-P&G 912 Cichladusa arquata Morning Thrush M-P&G 908

Dryocichloides bocagei Alexander's Ground Robin M-P&G 888

† Cossypha cyanocampter Blue-shouldered Robin Chat M-P&G 889

Modulatrix stictigula Spot-throat Mountain Robin M-P&G 894

Turdus fischeri Spotted Ground Thrush M-P&G 846 Phylloscopus budongoensis Uganda Woodland Warbler M-P&G 965

Cisticola bodessa Boran Cisticola M-P&G 1024
Cisticola ruficeps Red-pate Cisticola M-P&G 1043
Cisticola troglodytes Foxy Cisticola M-P&G 1038
Cisticola eximia Black-backed Cisticola M-P&G 1021
Heliolais erythroptera Red-winged Warbler M-P&G

Prinia somalica Pale Prinia M-P&G 1046

Apalis chariessa White-winged Apalis M-P&G 984

Apalis binotata Masked Apalis M-P&G 981

Camaroptera superciliaris Yellow-browed Camaroptera M-P&G 1012

Eremomela badiceps Brown-crowned Eremomela M-P&G 1007

Hyliota flavigaster Yellow-bellied Hyliota M-P&G 813 Hylia prasina Green Hylia M-P&G 1281

Pholidornis rushiae Tit Hylia M-P&G 1282

Muscicapa gambagae Gambaga Flycatcher M-P&G 778

Muscicapa sethsmithi Yellow-footed Flycatcher M-P&G 783

Myioparus griseigularis Grey-throated Flycatcher M-P&G 786

Artomyias fuliginosa Sooty Flycatcher M-P&G 804 Myopornis boehmi Boehmi's Flycatcher M-P&G 802 Fraseria ocreata Fraser's Forest Flycatcher M-P&G 800

† Batis Jiops Ruwenzori Puff-back Flycatcher M-P&G 815
Batis orientalis Grey-headed Puff-back Flycatcher
M-P&G 818

Erythrocercus livingstonei Livingstone's Flycatcher M-P&G 809

Erannornis albicauda White-tailed Blue Flycatcher M-P&G 827

Trochocercus cyanomelas Crested Flycatcher M-P&G 828 Anthus vaalensis Buffy Pipit M-P&G 705

Dryoscopus senegalensis Hartlaub's Puff-back (Shrike) M-P&G 1129b

Laniarius ruficeps Red-naped Bush Shiike M-P&G 1126 Laniarius leucorhynchus Sooty Boubou M-P&G 1122

† Malaconotus quadricolor Four-coloured Bush Shrike M-P&G 1142

Malaconotus cruentus Fiery-breasted Bush Shrike M-P&G 1146 A

Lanius souzae Souza's Shrike M-P&G 1111

Poeoptera lugubris Narrow-tailed Starling M-P&G 1208
Onycognathus fulgidus Chestnut-winged Starling
M-P&G 1200

Onychognathus salvadorii Bristle-crowned Starling M-P&G 1206

Lamprotornis chalcurus Bronze-tailed Starling M-P&G 1189

Lamprotornis aouticaudus Wedge-tailed Glossy Starling ؆Speculipastor bicolor Magpie Starling M-P&G 1187 Neocichla gutturalis White-winged Babbling Starling M-P&G 1183

Ø Spreo shelleyi Shelley's Starling M-P&G 1215
 Anthreptes anchietae Anchieta's Sunbird M-P&G 1276
 Nectarinia alinae Blue-headed Sunbird M-P&G 1267
 Nectarinia talatala White-bellied Sunbird M-P&G 1249

Nectarinia chalybea Southern Double-collared Sunbird M-P&G 1253

Nectarinia regia Regal Sunbird M-P&G 1259

Ploceus dichrocephalus Jubaland Weaver M-P&G 1325 ؆ Quelea erythrops Rcd-headed Quelea M-P&G 1361 Vidua orientalis Broad-tailed Paradise Whydah M-P&G 1445

Pyrenestes minor Lesser Seed-cracker M-P&G 1396, 1397

Nigrita bicolor Chestnut-breasted Negro Finch M-P&G 1387

Pytilia phoenicoptera Red-winged Pytilia M-P&G 1408 Estrilda perreini Lavender Waxbill M-P&G 1423

Lagonosticta larvata Black-faced Firefinch M-P&G 1416 Lagonosticta rara Black-bellied Waxbil M-P&G 1426 Ortygospiza locustella Locust Finch M-P&G 1404 Ortygospiza gabonensis Red-billed Quail-Finch M-P&G 1403

Emberiza cabanisi Cabanis' Bunting M-P&G 1467 Emberiza striolata House Bunting M-P&G 1477 Serinus gularis Streaky-headed Seed-eater M-P&G 1456 Serinus mennelli Black-eared Seed-eater M-P&G 1457 Linurgus olivaceus Oriole Finch M-P&G 1463

Many species in the list above are largely extra-limital.

Categories (3)—(10): For ease of reference, the categories are: (3) only indicative records, no precise egg-dates; (4) I to 5 definite dated records; (5) 6 to 10; (6) II to 20; (7) 2I to 50; (8) 5I to 100; (9) IOI to 500; and (10) over 500 definite dated records.

Species for which we have indicative or definite breeding records are listed hereunder in systematic order, since this simplifies cross-referencing. Following each species name (and its Mackworth-Praed & Grant number), the category in which it is found is indicated thus:

Balaeniceps rex Whale-headed Stork M-P&G 54 Category (3) and, where any exist, the total number of definite records is also given.

Non-Passeriformes

Struthionidae Ostriches

Struthio camelus Ostrich M-P&G 1 Category (9) 106 records.

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(b) central and southern. I, 3; II, 1;, III, 1; IV, 2;
VII, 5; VIII, 16; IX, 27; X, 18; XI, 3 . 76
All Region D. I, 4; II, 2; III, 2; IV, 2; VII, 5;
VIII, 19; IX, 27; X, 18; XI, 3; XII, 1 . 83
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Cards and an additional 34 records from Nairobi Park from L. Hurxthal provide a good enough series for Regions C and D to relate laying dates to climate reasonably well. The few records for Region A are also indicative. Hurxthal (PhD Thesis, unpub.) studied the Ostrich in the Nairobi Park, mainly from the viewpoint of survival, and found most of his nests from the air at peak breeding times, so that his records do not span the entire possible breeding season.

Ostriches lay a large clutch, over an average laying period of 17 days, and incubate for 46 days; so that, unless the clutch is incomplete, laying is dated some 30 days before the record. Ageing of chicks is very subjective as no good, wild, age-criteria have been published; we have discarded all records of large chicks. In some cases, ages of smaller chicks may have been underestimated. A few days after hatching (Hurxthal, pers. comm.), the chicks form into large flocks, composed of several broods; thus, broods of even small chicks may be aged at least 2½-3 months after the median laying date.

Both in Region D an in Region C, the peak laying period is August-October. Thomson (1885) made an omelette of ostrich eggs near Loitokitok (Region D) on 12 August 1883. In Region C all records indicate laying July-October, the dry season, while in Region D the peak August-October (63/84 records or 77%) is in the latter half of the mid-year dry season. Eggs hatching in November may be swamped by rains and the chicks die, or the nest deserted. Thus, nesting begins when the grass is tall and most chicks are hatched before the short rains begin. In the more arid parts of Region D, Tsavo Park, Meru, and Samburu, some breeding also occurs in the December-March dry season; this may be more pronounced north of Mount Kenya where the October-December rainy season may be the more regular of the two. In Region A, the few records suggest laying late in the dry season.

Thus, Ostriches generally lay in the dry season when their eggs are unlikely to be swamped by heavy rains. The growing young can often obtain fresh green food within one to three months of hatching; but more records may show that dry weather for the eggs is more important than green food for the small young.

Podicipitidae Grebes

Tachybaptus ruficollis Little Grebe M-P&G 4 Category (8) 79 records.

Data are adequate for Region D, where there is some breeding in almost every month, but a marked peak in and just after the long rains. This conclusion is locally supported in the Arusha National Park (Beesley 1973), and by the few results from Regions A, C and E, which are also in, or late in the rains. The results from Region B are biased by a single expedition by Pitman to Lake Bunyoni; and more data from this region may reveal a more widespread breeding season without such a marked peak in August-September. In Region C Reynolds (1968) observes that Little Grebes breed March-April near Tabora, late in the rains.

Observations indicate that, with the onset of heavy rain, Little Grebes rapidly spread from the larger lakes which are the main centres of population and take advantage of temporary ponds. If these last long enough they may breed there. A newly built dam in dry country will first be occupied by Little Grebes immediately after rains. Rain thus stimulates both local movement and breeding at main centres by this species. Evidently, when taking advantage of a temporary pond a new food supply is provided but whether there is any increase in the regular food supply in more permanent centres in the long rains, the peak breeding season, remains to be established.

It has been suggested to us (Diamond, pers. comm.) that dispersal during the rainy season to temporary ponds might just as well be an anti-predator reaction as an attempt to exploit a new food supply. We feel that this does not explain the similar peak of breeding observed on larger waters, where the threat of predators is likely to be more constant.

Podiceps nigricollis Black-necked Grebe M-P&G 3 Category (6) 18 records.

Region D. V, 1; VI, 11 +; VII, 4; VIII, 2. 18

The records suggest that this species breeds at the same time as *T. ruficollis*, mainly after the long rains.

Confusion of identification is possible in some cases, but not in recent records.

Podiceps cristatus Great Crested Grebe M-P&G 2 Category (8) 71 records.

Adequate records from Region D suggest that the breeding season is widespread in both dry and wet seasons, with peaks in or after both rains. The record of heavy November breeding in Region D is due to one visit to Lake Nakuru, where a large number of nests were found in one day, and is not necessarily typical. Unfortunately at Lake Naivasha where Jackson (1938) and Williams (1947) found evidence that most breeding took place May-July, this grebe has now been largely exterminated by gill nets. However, recent (1977) records included here show a clear peak June-August, suggesting that these earlier records from Naivasha are accurate.

Pelecanidae Pelicans

Pelecanus onocrotalus Great White Pelican M-P&G 31 Category (10) 172 660 + records.

Region C. VI, 40 000; VIII, 42 000 . 82 000 Region D. I, 200; II, 6200; III, 5170; IV 17 960; V, 9635; VI, 21 210; VII, 17 250; VIII, 1340; IX, 1300; X, 1925; XI, 8470; XII, 0. 90 660

Three cards used, and data from the literature (Vesey-Fitzgerald 1954, 1957; Thomas 1960; Brown & Urban 1969; Brown, Powell-Cotton & Hopcraft 1973) give a total of over 172 660 approximately dated records plus another 10 000 from Region D, which were spread over the months April-July (Lake Natron, 1962). In Region C, the Lake Rukwa colony, which has never been regularly monitored, even from the air, has, in several different years, bred largely June-August in the dry season, but apparently when the floodplain of the river is inundated. Most recent records from Region D come from Lake Elmenteita, where breeding was almost continuous from March 1968 to December 1970; and again occurred in 1973, 1974, 1975 and 1977. Recent records from here indicate some laying as soon as the long rains start in March, building up to a peak in April, continuing with a secondary peak June-July; and in some years continuing in the latter half of the year with another lesser peak in November. The laying peaks are in the rains and just after the long rains. Brown & Urban (1969) surveying breeding seasons known up to then, and including the 1962 Lake Natron breeding, concluded that inaccessibility was more important than dry or wet seasons, but the Lake Elmenteita site is absurdly accessible in relation to others known in East Africa or Ethiopia, and this suggests in recent years that breeding is triggered by the onset of rain.

However, very heavy rain causing a sharp rise in water level can also cause wholesale desertion, even by pairs not threatened, as happened to about 8200 pairs in two colonies in August 1977. In 1968, the initial breeding of pelicans was triggered by the presence of breeding colonies of Greater Flamingos, which the pelicans then virtually wiped out. Similar association with Greater Flamingos, resulting in destruction of flamingo colonies, was observed in 1969–71 (Brown, Powell-Cotton & Hopcraft 1973). From 1973–75 Great White Pelicans have also bred alone, beginning in April, with peak laying June-August after the long rains, in some years continuing later.

Great White Pelicans are thus irregular, highly opportunistic breeders whose laying may be triggered by, or whose colonies may desert en masse through the onset of rains, the availability of an inaccessible site, or by such curious features as the presence of a colony of other gregarious birds (flamingos). However, they are not always dependent on the same features even in the same site. Observations at Lake Shala, Ethiopia over 10 years (Urban & Jefford, in prep.) have shown that 3000-12 000 pairs may breed, with a consistent peak in the late dry season carrying over into the rains, cf. Lake Elmenteita with peaks late in the main rains continuing into dry seasons. There is thus no consistent pattern related to climate, and although the Elmenteita site is very easily accessible compared with most others known, it is still the most inaccessible available near the feeding area at Lake Nakuru. On available evidence, it is not possible to connect breeding with peak food supply demand (with large young) except to say that if the food supply fails, as at Lake Natron in 1962, breeding stops. In view of the extreme shyness of these birds at breeding colonies, inadvertent or deliberate human disturbance, including that by ornithologists (who in early years knew no better), can cause mass desertion to be followed perhaps by re-laying.

Pelecanus rufescens Pink-backed Pelican M-P&G 32 Category (9) 276+ records.

Numbers given are minimal; accurate counts of nests at different stages were seldom made by any observer, The best-known colony is at Rakewa, South Nyanza. Kenya, where about 250 pairs breed, but only about 20 were accurately dated (Burke & Brown 1970). This colony has not been subsequently monitored, but breeding begins in August, in the late rains, and ends in March in the late dry season, apparently consistently. Other observations from Region B tend to support these dates. From Region C the only record is in the height of the rains, and in Region D laying is in the long rains, breeding continuing into the dry season. From Region E Jackson (1938) gives breeding at Lamu in August, with young, suggesting laying in June, the same time as North (1939) found pelicans incubating on the Tana River.

Although the detail is inadequate, it appears that this pelican breeds late in the rains, and that its period of maximum food demand (with large young in the nest) occurs in the dry season throughout its range. Fish may be more readily caught in clear water by this species, which fishes alone and by stealth, as compared with the communal 'by touch' feeding methods of *P. onocrotalus* in which the clarity of the water matters little if at all.

Sulidae Gannets and Boobies

Sula dactylatra Masked Booby M-P&G 22 Category (10) 500-550 records.

The only recent good record is for Latham Island, in Region D but 60 km offshore (Gerhart & Turner 1978). They found 500-550 nests at all stages, from eggs to quite mature young, on 19 November 1971, but unfortunately provide no accurate details of different stages. This indicates that breeding might begin in early September, with the latest young leaving the nests about February. They summarise records by nine other persons or parties, from 1918-1972, recording an indefinite number, but thousands, of nests. These records again suggest that most breeding begins about September, laying perhaps peaks in October and early November and large young fledge from late nests in February. A visit by L. P. Lane on 18 February 1944 recorded breeding but while 5000 birds were present at dusk only 200 were there at 10.00 hrs on 19 February, suggesting that most birds present could fly. On the other hand, a visit by V. G. Glenday on 19 March 1951 found 1000-2000 birds nesting, many nests containing newly hatched young, suggesting laying January-February. This perhaps indicates breeding by a new group, following completion by others, as happens with several of the species of Pelecanidae. However, this is conjectural, and only systematic visits throughout the year can show whether breeding peaks, as seems likely, September-November, when the southeast moonsoon is over and the seas are generally calm. Latham Island is always rather inaccessible and apparently entirely so by boat during the monsoon; however, aerial surveys would soon reveal additional facts.

S. leucogaster, the Brown Booby, is also reported to breed on Latham Island, but Gerhart & Turner (1978) dismiss all these possible records as immatures of S. dactylatra.

Phalacrocoracidae Cormorants

Phalacrocorax carbo (incl. lucidus) Cormorant M-P&G 25 Category (10) 815+ records.

The records are adequate to demonstrate that both on Lake Victoria and on alkaline and fresh lakes of the Rift Valley (Naivasha, Nakuru) cormorants breed practically all the year round. On Lake Victoria records are split about evenly between wet and dry months in Region B, but the single record for Region C is late in the rains: In Region D there are more records in dry than in wet months, but colonies were often not accurately counted. A colony at the mouth of the Njoro River on Lake Nakuru has been continuously occupied from 1961 to date, but has never been regularly monitored to determine breeding peaks. Despite a large number of records, the result is thus rather unsatisfactory. Most early records are for one or two clutches taken from larger colonies.

More regular and thorough monitoring of larger colonies may reveal peaks in the rains on Lake Victoria and elsewhere. On Lake Victoria protracted breeding seasons may be in part due to a lack of suitable sites, so that as early nesters complete their cycle fresh groups occupy the same sites (Marshall & Roberts 1959). However, this does not explain every situation, even on Lake Victoria. Ability to breed in most months of the year without any very obvious peaks suggests, however, that food supply is adequate at any season.

Phalacrocorax africanus Long-tailed Cormorant M-P&G 27 Category (10) 1493+ records.

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Region B. I, 10; II, 10; III, 4; IV, 17; V,
74; VII, 112; VIII, 123; IX, 444;
X, 250; XI, 100; XII, 55 . . . 1199
Region C. IV, 100+; also II-IV . . 100+
Region D. I, 42; II, 35; IV, 2; V, 75+;
VI, 5; VII, 2; VIII, 2; X, 1 . . 164
Region E. IV, 30 . . . . 30
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Again numbers are minimal, as some early records refer to one or a few clutches from large colonies. However, as Jackson (1938) observed, this species breeds on Lake Victoria most of the year, but apparently with a pronounced peak July-November, late in the rains or early in the dry season. The Region C records from Lake Victoria are for the height of the rains and it is also recorded breeding in the Wembere heronry (no numbers) in the height of the inundation season; the same applies to the single record from Region E. In Region D breeding is quite widespread, but at Lake Naivasha, at least, there is a peak in May, late in the long rains.

Thus, where there are more definite rainy and dry seasons, this species tends to breed in the rains, but in the more equable two-season climate of Region B peak breeding is at the end of the rains and early dry season. As in *P.carbo* Marshall & Roberts (1959) found new groups occupying nests vacated by earlier breeders but this does not occur everywhere on Lake Victoria or elsewhere. More records from southern Lake Victoria would be valuable for comparison with Region B. Since this species feeds on the always abundant small haplochromid fish in Lake Victoria, no obvious connection with food supply is possible.

Anhingidae Darters

Anhinga rufa Darter M-P&G 28 Category (10) 899 records.

Region A. I, 1; II, 5; III, 5; VI, 40; VII.	
70; IX, 18	139
Region B. I, 40; II, 9; III, 5; IV, 12; V, 4;	
VI, 7; VII, 5; VIII, 320; IX, 28; X, 20;	
XI, 12; XII, 24	486
Region C. V, 1: (Also recorded with eggs	
III, IV: young IV)	I
Region D. I, 20; II, 5; III, 17; IV, 10; V,	
21; VI, 40; VII, 27; VIII, 40; IX, 38;	
X, 3; XI, 5; XII, 6	232
Region E. IV, 40; VIII, 1	41

The 899 available East African records, mainly from Lake Victoria and Lake Naivasha, are not fully representative of the numbers seen, since old records are often of 1-3 clutches from a much larger colony though one is for a colony of 300 nests in Region B. Where records are adequate (Regions B and D) some breeding occurs in almost any month, usually associated with cormorants, herons, or ibises. Breeding may be irregular, e.g. at Lake Baringo it does not occur annually in the same sites. Here, there is a marked peak June-September, a drier interval between the rainfall peaks. In Region B (Lake Victoria) there is a marked peak September-January, late in the rains and in the dry season; at Lake Naivasha most records are for June-September, a cool dry season. The records for Regions C and E indicate breeding at maximum inundation, as with other species in the Wembere and Garsen heronries.

The records tend to show that the Darter avoids breeding in the wettest seasons, but in Regions C and E breeds when other associated species breed, at the height of inundation periods. The Darter's mode of fishing, by slow underwater stalking of prey, may favour fishing in clear water, and hence breeding in drier periods. However, at Lake Nakuru, with opaque water, it breeds all the year round in association with cormorants.

Ardeidae Herons, Bitterns, Egrets

Ixobrychus minutus Little Bittern M-P&G 50 Category (4) 4 records.

Jackson (1938) states that it breeds at Entebbe March-July and November-December and at Naivasha May-June. The few dated records suggest that the breeding season is extended, perhaps with peaks in the rains.

Ixobrychus sturmii African Dwarf Bittern M-P&G 51 Category (4) 3 records.

The few definite records all suggest laying in or just after the main rains.

Nycticorax nycticorax Night Heron M-P&G 48 Category (9) 266 records.

 Region A. II, I
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 Region C. II, 21; III, 1; IV, 1
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The figures in several cases represent only a fraction of the numbers seen; colonies are from 1–1000 pairs (Wembere, Tanzania). With one exception all breeding is in the rains, either in the height of, or late in, the main rains. Late colonies may be associated with flooding rather than actual rainfall (Tanzania and Region E). Breeding is irregular, not occurring annually in the same localities. The single record for Region A is late in the dry season.

Nycticorax leuconotus White-backed Night Heron M-P&G 49 Category (4) 3 records.

The few definite records all indicate laying in or just after the main rains.

Ardeola ralloides Squacco Heron M-P&G 43 Category (10) 1373 records.

The larger figures are broad estimates rather than accurate counts. All records indicate laying in the rains, peaking at the height of the rains or, in inundated areas (Wembere; Garsen) late in the rains at the height of flooding.

Ardeola rufiventris Rufous-bellied Heron M-P&G 47 Category (4) or (5) 1 record: 8 pairs.

Region B. IV, 1; a small colony of 8 pairs in Busi Swamp, Uganda. The record is actually for May, but the single clutch taken was heavily incubated and eggs would have been laid in April, in the long rains.

Bubulcus ibis Cattle Egret, or Buff-backed Heron M-P&G 42 Category (10) 11 315 records.

Region B. III, 5; IV, 360; V, 198; VI, 35;
IX, 81; X, 71; XI, 10; XII, 5 . . . 765
Region C. I–II, 10 000 10 000
Region D. III, 30; V, 45; VI, 150; VII, 25 250
Region E. V, 300 300

The 11315 records are not based on complete counts except in a few cases in Region B. Colonies are from a few pairs to 10 000 (Wembere, Tanzania). The Cattle Egret breeds mainly in or just after the main rains, or in inundated areas when flooding occurs. On Lake Victoria there is a

marked secondary peak September-October, at the end of the rains. In Region D most breeding is after the long rains extending into the dry season. This terrestrial feeder is perhaps less directly affected by rainfall than some others, but usually breeds mainly in the rains in association with other herons and sometimes *Phalacrocorax africanus*.

Butorides striatus Green-backed Heron M-P&G 45 Category (7) 32 records.

Of the 32 records, 27 are from Lake Victoria, Region B. This species breeds singly or in small loose groups, with a rather diffuse breeding season, 7/12 months in Region B. Here there is a marked peak in the main rains April–May (16/27 records) and a possible minor peak in August, which may be largely fortuitous. Although it does not normally breed in dry seasons in Region B, the few records for Regions C and D are in dry months or at the end of the rains.

Egretta ardesiaca Black Heron M-P&G 39 Category (9) 102+ records.

Region B. III-VI. r + r + Region C. I, 10; II, 30; IV, r + 41 + Region E. V, 30; VI, 30 60

Jackson (1938) gives breeding March-June in the old Kisumu Heronry; there are no recent records from Lake Victoria. Breeding in Regions C and E is at the height of the flood in the Wembere and Garsen heronrics. This heron evidently breeds at the height of rains or flood like others.

Egretta alba Great White Egret M-P&G 37 Category (10) 583+ records.

 Region A. II, 5+; III, 5+
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 10+

 Region B. IV, 203; V, 93; VIII-IX, 165
 461

 Region C. I, 50; II, 53
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 Region D. VII, 5
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 Region E. V, 4
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Most records are from Region B, in the Kisumu heronry, where it breeds in the height of the rains or (August-September) in response to adventitious flooding. In Regions C and E, at the Wembere and Garsen heronries, records are for the height of flooding. The records for Region A are from Lake Baringo, in the hot dry season and for Region D in the cool dry season. This species thus breeds mainly in the rains or height of flood, but breeding is irregular, not occurring every year in the same locality (Kisumu) and may start, with birds gathering and building nests, but not persevering. Jackson (1938) gives breeding in unspecified numbers March-June in the old Kisumu heronry, dates which agree with more recent records.

Egretta intermedia Yellow-billed Egret M-P&G 38 Category (9) 338+ records.

Some figures are careful estimates, others an odd clutch from a larger colony. Jackson (1938) gives breeding March-June in the old Kisumu heronry which agrees with more recent data, and at Naivasha, no date, but probably June. All recent records from Regions A and B indicate laying at the height of the rains and in Regions C and E at the height of inundation or floods. In Region D recent records from Manyara and Ngorongoro indicate breeding after either long or short rains. Like others, it is an irregular breeder, not laying every year in the same localities; in 1975–76 birds gathered at Kisumu heronry in April but did not lay.

Egretta garzetta Little Egret M-P&G 40 Category (10) 1700 records.

On Lake Victoria the main breeding is at the height of the long rains April-May; Jackson (1938) gives March-June for the old Kisumu heronry. Some breeding also occurs September- December, after the rains; breeding is irregular, more than 150 pairs sometimes beginning to nest, but deserting if rains or flooding do not persist. The records for Region C are mainly from the Wembere heronry, at the height of inundation, but include records October-December from Mafia Island. Those for Region E are mainly from Kisite Island near Shimoni, and suggest continuous breeding December-July, peaking in February (dry) and April-May (wet). These records suggest that coastal birds are not confined to wet season breeding, but can have an extended breeding season. The Mafia records fit in with this rather than the other Region D records, which are mostly for the cool dry season.

Ardea cinerea Grey Heron. M-P&G 33 Category (8) 51 records.

Region A. Young at various stages in VII suggest laying V-VI.

A very irregular, erratic breeder, perhaps most regular in Region E. Does not breed every year in some localities, e.g. no records at Naivasha 1970-76 after breeding in 1969.

Available records suggest breeding in the height of the rains in Regions A and C like other herons; in Region D nesting in late rains or just after, with a second peak late in short rains. Region E coastal records show both dry and wet season breeding; food may be available in any month. At Garsen breeding is in the height of inundation.

Ardea melanocephala Black-headed Heron M-P&G 34 Category (10) 3790 records.

Region A. II, 15; IV, 12; V, 1	28	
Region B. I, 15; II: III, 55; IV, 785; V,		
345; VI, 61; VII, 1; VIII, 145; IX, 91;		
X, 10; XII, 1	1509	
Region C. I-II, 35; IV, 30	65	
Region D. (a) Other than Nairobi: II, 12;		
III, 30; IV, 152; V, 5; VI, 15; VII, 13;		
VIII, 6; IX, 10; X, 2	245	
(b) Narobi heronry: I, 35; II, 87; III,		
171; IV, 432; V, 187; VI, 195; VII, 132;		
VIII-IX, 152; X, 114; XI, 220; XII,		
136	1861	
All D. I, 35; II, 99; III, 201; IV, 584; V,		
192; VI, 210; VII, 145; VIII-IX, 168;		
	2106	
Region E. X, 48; XI, 26; XII, 8	82	
3		

The best documented of all East African species, and of special interest because of (a) its habit of breeding in towns or near human habitations and (b) a detailed study at Nairobi, where it bred continuously for two and probably more years.

Records for Region A suggest breeding in the rains or at the end of the long dry season. In Region B most records are for the Kisumu heronry, where there is a very clear peak April–May, the height of the rains, and one record of a colony laying August–October after unusual rains. However, in this region it is stated by Jackson (1938) and Pitman (cards, Uganda) to breed October–May continuously (dry season and into the rains); the figures for these months are only a small sample of much larger colonies in Entebbe and Kampala. Region C records show that it breeds in the rains like other species in the inundated Wembere Steppe, and even in towns nest repair was in progress October–November, at the beginning of the rains, suggesting main breeding in the rains. One record from Shinyanga is, however, early in the dry season (April).

In Region D the records from elsewhere broadly confirm the data from the Nairobi heronry, with a peak in the main rains but an extended breeding season with some nesting in most months. Better records from some other known town heronries would probably emphasise this point. At Nairobi, where the herons are virtually terrestrial feeders, there is a peak in and just after the long rains, and a secondary peak in the short rains, November. In fact, the details of the study (North 1963) show that the greatest numbers are associated with the heaviest rains; in 1961 the short rains were heavier than the long rains and the herons reached a high peak of breeding numbers, 170 occupied nests in November cf. about 35 in April.

Breeding was not recorded in Region E until 1976, when a colony of over 80 pairs developed in Malindi Township. Breeding here clearly peaked October—early November, in dry warm weather after the main rains; but this colony was unoccupied in 1977.

It seems possible to draw the tentative conclusion that those populations of this species dependent on an aquatic environment and a fish or amphibian diet (e.g. the Kisumu heronry) lay in the rains like other herons and will often abandon their nests if rains fail, or breed irregularly according to the intensity of rains and floods. On the other hand, most known colonies in towns or near human habitations seem to have an extended breeding season, perhaps all the year round, but often with a peak in the rains (when both fish and large insects are most abundant). One coastal colony, however, peaked well after the rains. More studies of other town heronries are needed to ascertain the point (e.g. in Kampala, Entebbe, Njoro, Kakamega, etc.). Town heronries in Tanzania may prove an exception to this generalisation, and may only be active in, or late in the rains.

Ardea goliath Goliath Heron M-P&G 35 Category (8) 81+ records.

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Region A. II, 7; IV, 9; V, 6; VI, 4; VII, 6;
VIII, 6; X, 1; XI, 9; XII, 2. . . 50
Region B. IV, 1; VIII, 2; IX, 2. . . 5
Region C. I, 2; VI, 1+. . . . . 3+
Region D. II, 4; III, 2; IV, 5; VI, 4; VII, 2;
IX, 2; X, 2; XI, 1; XII, 1. . . . . . 23
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This great heron, although apparently entirely dependent on fish, has the most elastic of any heron's breeding season, with some records for every month in East Africa and, in the regions where there are adequate records for analysis (A and D), breeding in 9/12 months in each. In Region A there is a slight peak in the main rains (April-June); but most of these records are from Lake Baringo, one of the few places where this heron breeds in small colonies of up to 10 pairs. There are rather few records for the dry season November-March (12) compared to the wet, April-October (32), indicating a preference for breeding in the rains. In Region D there is a marked peak at Lake Naivasha April-June (9/23 records) indicating breeding in or just after the long rains for preference. The few records for Region B are in wet or partly wet months, and for Region C both in dry and wet seasons; however, these are too few to be truly indicative.

Ardea purpurea Purple Heron M-P&G 36 Category (9) 159+ records.

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Region A. II, 2+; III, 2+; IX, 14 . . . 18
Region B. II, 4; III, 18; IV, 44; VI, 1 . . 67
Region C. IV. (Wembere) . . . .
Region D. II, 22; VI, 1; X, 1 . . . 24
Region E. IV, 40; VI, 10 . . . 50+
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Most records indicate a peak of breeding at the height of the rains, or in inundated areas (Garsen). At Lake Baringo there is apparently a secondary peak in September in some years. Breeding is irregular, not observed in all years, even in apparently favourable habitat (e.g. Lake Naivasha). Jackson gives breeding January–March near Entebbe (end dry season). In the Wembere heronry of Tanzania breeding is recorded in April, at end of rains and inundation. This species appears generally dependent on rain for successful breeding, with some exceptions.

Balaenicipitidae Whale-headed Stork

Balaeniceps rex Shoebill or Whale-headed Stork M-P&G 54 Category (3).

The single nest record card, for a pair with two young, apparently out of the nest, in Rwenzama Swamp, near Rwenzori National Park is for Sepember. With a breeding cycle of at least 130 days from laying to fledging (Buxton et al. 1978) this could mean laying in April. Jackson (1938) states that it breeds on Lake Kyoga March-June, in the long or main rains. Both in the Bangweulu Swamps, Zambia, and in the Nile Sudd, Sudan, eggs are laid in the dry season, and young fly late in the dry season or early in the rains (Buxton et al. 1978; A. Guillet, pers.comm.)

Scopidae Hamerkop

Scopus umbretta Hamerkop M-P&G 53 Category (7) 23 records.

Despite its abundance and wide distribution good definite records of breeding are scarce. Most accurate dates depend on egg-collectors and the few good records reflect the difficulty of correctly ascertaining the nest contents. The definite records suggest a rather elastic breeding season, with more records (16/23) in dry periods than in rains. This would be surprising and may be misleading in view of what is known of the food of this species (frogs, tadpoles, small fish). More definite records are badly needed: a full study of the Hamerkop is long overdue.

Ciconiidiae Storks

Ciconia abdimii Abdim's Stork M-P&G 58 Category (6) 14+ records.

In our area breeds in small colonies in western Kenya and Uganda, beginning in January and continuing to lay until May. Nesting begins in the dry season and runs into the early rains. The sole record for Region D is of a colony in northern Turkana on a rocky cliff, of about 20 pairs, of which several (estimated here at 5+) had laid in June, a dry season, but corresponding to laying or breeding in the Sudan.

Giconia episcopus Woolly-necked Stork M-P&G 57 Category (4) 5 records.

All laying dates are in the dry season; nothing is known about breeding in Region E where this stork is commoner than elsewhere.

Ephippiorhynchus senegalensis Saddle-billed Stork M-P&G 60 Category (6) 13 records.

Region A. I, 1; X, 1 .		2
Region B. IV, 1; IX, 1 .		2
Region C. IV, 1; V, 1; VI, 3		5
Region D. IV, 1; V, 3 .		4

Records show that this stork can breed either in dry or wet seasons. In Region C with the most records (5) the dry season is preferred, but in Region D a peak in the long rains is indicated. Both suggest, however, that young would mature and leave the nest towards the end of a dry season, as laying in April–May in Region D would produce fledged young August–September, just before the short rains.

Anastomus lamelligerus Open-billed Stork M-P&G 59 Category (10) 2520+ records.

Region B. I, 46; III, 102; IV, 18; V, 42;
VII, 2; IX, 40; X, 30; XII, 70 . . 350
Region C. I–II, 2000; IV, 2+; XII, 8 . 2010+
Region D. VI, 160 160

With some exceptions this stork breeds at the height of the rains or in maximum inundation periods (Wembere, Tanzania). The exceptions are odd records for July in Region B, and 160 pairs in Region D in Tanzania in June (dry). Breeding near Kisumu occurred in September-October 1975 and again December-January 1976, probably in response to unusual conditions, in inundated Acacia trees.

In Region E for which there are no accurately dated records, North (1939) records several hundred pairs in August, suggesting laying in June, at the height of the inundation at Garsen; and L.H.B. in 1962 saw large numbers near the Garsen heronry in March, when they had not yet laid. Kahl (1968) has suggested that laying in the rains is connected with the emergence, with rains, from aestivation of the snail *Pila* sp. which is one of the main foods.

Leptoptilos crumeniferus Marabou Stork M-P&G 61 Category (9) 475 + records.

The data from Regions A, B and C all confirm Kahl's (1966) observation that Marabous breed mainly in the dry

season, with odd late nests, probably re-laying, in which young are reared in the rains. In Region D, where the entire breeding season of more than 120 days between laying and first flight cannot be completed in any one season, there are conflicting peaks in July (dry) at Arusha Chini, and in November (one of the wettest months) on the Tana River and further north. This suggests that in areas where there is a clear alternation between dry and wet seasons (which applies to Region B more clearly than to Region D) the Marabou breeds in the dry season, but it can also breed successfully in wet weather where short (3 month) dry and wet seasons alternate. In fact, laying along the Tana River in November would ensure that the young left the nest about March, just before the long rains, and most of the breeding season, with maximum food demand for the young, would be dry.

Mycteria ibis Yellow-billed Stork M-P&G 62 Category (10) 2766+ records.

This stork has an absolutely clear preference for breeding at the height of the rains, beginning rather early and reaching a peak in the heaviest rainfall months, or in maximum inundation (Wembere, Tanzania). In Region D, where the alternation of seasons is somewhat less clear, there are a few records late in the rains or early dry season; however, it is not a common breeder here. It feeds much on frogs, which emerge after rain, and also fish in shallow muddy water.

Threskiornithidae Ibises and Spoonbills

Threskiornis aethiopica Sacred Ibis M-P&G 63 Category (10) 6008 + records.

In several cases, records are for a small sample of a much bigger colony. However, it is clear that the Sacred Ibis breeds mainly at the height of the rains or at periods of maximum inundation (Wembere, Region C and Garsen, Region E), tending to build up to peak laying a little late in the rains and, in some areas (Region D), continuing to breed into the cool dry season in July. Laying August-September, probably in response to unusual flooding, occurred one year near Kisumu (Region B). It thus appears to resemble the Yellow-billed Stork, Open-billed Stork, and several herons in its peak breeding requirements. However, it is a very irregular breeder and may abandon a colony

without completing the cycle for reasons still obscure, both in Kenya and Ethiopia (Urban 1974).

Bostrychia hagedash Hadada M-P&G 65 Category (8) 71 records.

Where records are adequate they show that this solitary ground-feeding ibis breeds in every month, but with a peak in and just after the long rains. In Region B 27/50 records are March-May with a second peak in June. The few records for Regions C & E are, however, in dry months.

Bostrychia olivacea Green Ibis M-P&G 66 Category (3).

The only record is that of Akeley, quoted in Jackson (1938) without dates, but possibly laying between June-August. The species is rare and has not been observed breeding since 1910.

Plegadis falcinellus Glossy Ibis M-P&G 68 Category (9) 212+ records.

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Region B. VII, I . . . . . I Region C. IV, 170+ . . . . . . 170+ Region E. V-VI, 40; VIII, I . . . 41
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This species clearly breeds late in the rains wherever it is known. Jackson (1938) writing of the old Kisumu heronry, says that it arrived later than other species and did not breed till July, at the end of the main rains. Both in the inundation zone of the Wembere Steppe and the Garsen heronry the records indicate laying late in the inundation period. Whether this unusual breeding peak, later than in any of the other herons and ibises with which it associates, is regular and connected with food, remains to be discovered. It might also be due to inability to compete with larger, more numerous species (Reynolds, pers. comm.)

Platalea alba African Spoonbill M-P&G 70 Category (10) 1220+ records.

The African Spoonbill breeds normally in or late in the main rains, and in inundated areas (Wembere, Garsen) rather late in the inundation period, resembling the Sacred Ibis. In Region D it has a much more elastic breeding season, including dry months, peaking in the long rains, continuing into the cool dry season June–July, and with a

second peak in the short rains November-December observed at Ngorongoro. Although it thus shares the habits of most large water birds in breeding chiefly in the rains, it is somewhat more adaptable than some other herons, storks, or ibises.

Phoenicopteridae Flamingos

Phoenicopterus ruber Greater Flamingo M-P&G 71 Category (10) 77 915 records.

Numbers in some sites can only be approximations, but at Lake Elmenteita and Nakuru are probably accurate to within 10-15%. Breeding can occur in most months of the year, but appears to be triggered by different factors at Lakes Elmenteita, Natron and Magadi, the only sites known. At Lake Elmenteita the earliest breeding occurs March-April, following the onset of the long rains. There is a secondary peak June-July, which can be due to later breeding or to failure (often complete) of earlier colonies, or to new occupation of an existing colony by birds which hitherto could not find space. In a few years breeding occurs also in the short rains October-December (especially 1956). Although, at Lake Elmenteita, breeding thus may be triggered by rainfall, in good breeding years it continues into the cool dry season, and sometimes starts then. Also, in recent years, attempts to breed by Greater Flamingos at Lake Elmenteita have been disrupted by Marabou Storks and by competition for space from Great White Pelicans; both may have substantially affected flamingo breeding behaviour (Brown, Powell-Cotton & Hoperaft 1973, Brown 1958).

At Lakes Natron and Magadi, Greater Flamingos usually breed in colonies of Lesser Flamingos *Phoeniconaias minor*. The largest colonies (10 000 + pairs) were admixed with the huge 1962 Magadi colony of Lesser Flamingos. However, a very large colony of Greater Flamingos alone also occurred in February 1962 at Lake Natron, and others may have been overlooked. February is in the height of the hot dry season but most of the colonies at Lakes Natron and Magadi have been in August-November, the end of the cool dry season and into the short rains, which are light in this area.

On present evidence, although there is some correlation between onset of breeding and rains at Elmenteita, it is impossible to formulate sound conclusions on the relation between climate, food supply, and breeding dates. Greater Flamingos can also be triggered to breed by the presence of colonies of Lesser Flamingos, and likewise can trigger the breeding of Great White Pelicans, which subsequently destroy the flamingo colonies by taking over the breeding slands.

Phoeniconaias minor Lesser Flamingo M-P&G 72 Category (10) 3 320 000.

Region D only. Lakes Natron and Magadi; I case from Lake Turkana (Rudolf).

I, 50 000; II, 30 000; III, 45 000; VI, 30 000; VII, 710 000; VIII, 1 040 000; IX, 100 000; X, 590 000; XI, 560 000; XII, 165 000 . . . 3 320 000

While numbers are approximations, they are not mere guesses but based upon methods of counting from the air and sample densities in colonies (Brown & Root 1971). All records apart from 30 000 at Lake Turkana in June 1957 are for Lakes Natron and Magadi. Here there is a main breeding peak observed over several years October-November, sometimes continuing into December and even January, in the short rains. This peak is distorted by the enormous 1962 Magadi colony in which peak laying was in August, the cool dry season. Lesser Flamingos do not breed every year; regular observations maintained in 1953-62 showed some breeding in 7/10 years, but by only about one tenth of the total population/year on average. Available evidence does not permit a clear correlation between climate, food supply and breeding season, but most breeding occurs in the four months August-November inclusive, late in the cool dry season and into the short rains. Colonies occurring at Lake Natron January-March are either the late remnants of large earlier colonies (January 1961), or are likely to fail.

These figures do not include sporadic egg-laying at Lakes Bogoria (Hannington), Nakuru, or occasionally elsewhere, as these small-scale sporadic layings are normally abandoned before hatching and are not therefore considered true breeding attempts.

Anatidae Ducks and Geese

Dendrocygna bicolor Fulvous Whistling Duck. M-P&G 95 Category (5) 6+ records.

Also reported to breed in Region B May-June, but no recent confirmation. This duck appears to be mainly a non-breeding migrant but records from Region C (many) appear definite. Mistaken identity of eggs or young may be suspected in Regions D and E; in the latter, Jackson (1938) reported breeding on the same islands as D. viduata, but on the evidence of his collector.

Dendrocygna viduata White-faced Whistling Duck M-P&G 94 Category (6) 20 records.

act 94 Category (b) 20 record	J.			
Region A. VIII, 2; XII, 1				3
Region B. VI, 1; XII, 1 .				2
Region C. V, I				I
Region D. I, 1; III, 1 .				2
Region E. VII, 6; VIII, 2; X	, 1; X	[, ι; λ	ΙΙ,	
2				12

Most records are from the coast where there is a definite peak July-August, a cool dry season. In other regions the scanty records suggest more breeding in dry than in wet months.

Alopochen aegyptiacus Egyptian Goose M-P&G 99 Category (9) 181 records.

In all regions the Egyptian Goose breeds in most months with no very pronounced peaks. Records for dry or mainly dry (120/180) months however, greatly exceed those for wet months. Most records are, however, for broods rather than eggs and age estimates may be subject to error. Since this goose largely feeds on waterside grass, normally green, there is no reason why any pronounced peak in laying dates should be observed.

Plectropterus gambensis Spur-winged Goose-M-P&G 100 Category (7) 23 records.

Most records are for broods, hence difficult to date accurately. The records from Region D suggest peak breeding in and just after the long rains. One record from Tanzania (Region C) suggests breeding about September, and Mackworth-Praed & Grant (1957) state that it breeds in Uganda in almost any month, without giving definite details.

Sarkidiornis melanotos Knob-billed Goose M-P&G 98 Category (5) 7 records.

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      Region B. VIII, 1
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Records are too scanty to be more than indications, but those for Region C (in literature) suggest breeding towards the end of the main rains.

Nettapus auritus Pygmy Goose M-P&G 97 Category (5) 8 records.

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Region B. I, 1; VI, 2; VII, 1; X, I . . . 5
Region C. VI, I . . . . . . . I
Region E. VII, 2 . . . . . . . . 2
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All the scanty records suggest breeding in dry seasons or in dry periods of an extended rainy season (June-July Region B). Stated to breed in Region E May-June (Jackson 1938) and on Pemba Island July and August (Mackworth-Praed & Grant 1957); the latter is supported by two recent records from Region E.

Anas sparsa Black Duck M-P&G 84 Category (6) 19 records.

Most records are for dry months (13/19) which is appropriate for a species largely inhabiting rivers liable to flooding.

Anas capensis Cape Wigeon M-P&G 89 Category (7) 37 records.

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Region C. VI, 1; VII, 4; VIII, 1 . . . 6
Region D. I, 1; III, 1; V, 7; VI, 7; VII, 3;
VIII, 6; IX, 3; X, 3 . . . . . 31
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All records from Region C are for the dry season; peak laying in Region D is late in or after the long rains, but 24/31 records are for dry or predominantly dry months.

Anas undulata Yellow-billed Duck M-P&G 83 Category (7) 22 records.

Most of the records are for the relatively cool dry period after the long rains in Regions B and D, and the only record for Region A is also in a drier break in the main rains.

Anas erythrorhynchos Red-billed Duck M-P&G 91 Category (7) 31 records.

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Region C. III, 1; IV, 2; V, 3 . . . . 6
Region D. I, 2, III, 1; IV, 1; V, 5; VI, 8;
VII, 5; VIII, 3 . . . . . . . . . . . . . 25
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Most records from both regions indicate peak laying at the end of and just after the main rains, extending into the cool dry season in Region D.

Anas hottentota Hottentot Teal M-P&G 90 Category (5) 7 records.

Netta erythropthalma Southern Pochard M-P&G 77 Category (6) 17+ records.

Records for all regions, though scanty, indicate laying late in or just after rains. Jackson (1938) states broadly that it breeds May–July in Region D (late rains—dry) and March–June and November in Toro (rains or dry). This duck may have been a more abundant breeder formerly than it appears to be at present.

Oxyura maccoa Maccoa Duck M-P&G 73 Category (5) 6 records.

The few records suggest an extended breeding season in both wet and dry seasons, more in dry than wet (5/6 records). Mackworth-Praed & Grant (1957) give May-July and October-January for Region D and May-June for Region C.

Thalassornis leuconotus White-backed Duck M-P&G 74 Category (7) 41 records.

The species has an extended breeding season, apparently peaking (24/40 records) late in the long rains and in the cool dry season in Region D. The young are dependent on Chironomid larvae for food; these are probably abundant in lakeside mud at most times. An extended breeding season is not therefore surprising.

Pandionidae Osprey

Pandion haliaetus Osprey M-P&G 186 Category (2).

The sole literature record, repeated indiscriminately from book to book, is that of Loveridge (1922). This is a bald statement, lacking any supporting detail, and runs: 'The Osprey was found nesting at Lake Naivasha with young on 16/VII/15'.

Since (i) there have been no more recent definite records here or elsewhere in East Africa; (ii) in 1915, there were no fish in Lake Naivasha other than the small minnow Aplocheilychthys antinorii (Tilapia spp. having been introduced after 1920, I.S.C. Parker, pers. comm.); and (iii) elsewhere, the Osprey feeds almost entirely on sizeable fish (99% or more), we consider that, at that time, it would have been impossible for an Osprey to breed at Lake Naivasha and reject this record as invalid, possibly due to mistaken identity. It is the more unlikely since, although conditions for breeding (food supply and suitable breeding habitat) are fulfilled elsewhere in Kenya, notably on the Coast and Lake Victoria, there have been no good records or any indication of breeding at these more probable localities. Chorley (1938-40) claims to have found a nest built in November on Lake Victoria, but provides no proof of breeding. The case is analagous to the contested records of the Common Sandpiper Actitis hypoleucos breeding at Entebbe; but it appears easier to reject outright.

It has bee repeatedly rumoured recently that Ospreys breed on Lake Naivasha and on Lake Turkana (Hopson & Hopson 1975) but there is no definite evidence. Accordingly, we consider that there no definite breeding records of the Osprey in East Aftica.

Accipitridae Diurnal birds of prey

Aviceda cuculoides Cuckoo Falcon M-P&G 130 Category (4) 1 record.

Region D. XI, I I

The single definite record is that of Brown & Bursell (1968) with eggs laid in November (rains) in Region D. Cuckoo Falcons are common on the Kenya Coast August-September, and may be mainly migrants in Kenya.

Macheirhamphus alcinus Bat Hawk, M-P&G 134 Category (5) 6 records.

Most records are at the end of or just after the long rains. All but one (from Kampala) are from Dar es Salaam or Pemba Island. Although Bat Hawks occur elsewhere, they appear commonest along the coast.

Elanus caeruleus Black-shouldered Kite M-P&G 133 Category (8) 54 records.

Black-shouldered Kites breed in both dry and wet months, almost equally divided (26/28). Closer examination suggests that there may be peaks in the late rains and early dry season, when the grass is long and rodents and grass-hoppers abundant. In Region D, with 30/54 records, there is a marked rainy season peak April-May, with reduced breeding later in the year and a subsidiary peak in February (dry) and with the long grass largely burned. Since rodents may be abundant but hard to catch in long grass, further specific studies are needed to show whether breeding seasons are closely related to the availability of rodent prey.

Chelictinia riocourii Swallow-tailed Kite M-P&G 131 Category (3).

This kite is only known to breed in the northern arid parts of Region D. Although there are no definite dated records, all observations indicate laying in late April or May, the height of the main rains. One card reports frequent copulation in Turkana on 10 April, and M.E.W. North (in litt.) reported breeding north of Marsabit in May. This largely insectivorous species apparently breeds in the rains throughout its range.

Milvus migrans Black Kite M-P&G 132 Category (8) 86 records.

		XI-II
Region A. I, 3; II, 8; III, 1; IV, 1; XI,		
ı; XII, ı	15	14
Region B. I, 6; II, 2; III, 12; VI, 2; IX,		
4; X, 1; XI, 5	40	25
Region C. IV, 1; XI, 2; XII, 1	4	3
Region D. I, 4; II, 3; III, 4; V, 1; VII,		
1; VIII, 1; IX, 1; X, 2; XI, 6; XII, 2	26	19
Region E. V, I	I	
	86	61

This species is mainly a migrant, arriving from the north in October, breeding and departing northwards March-April. Its breeding season is clearly connected more with this migration pattern than any other factor, 61/86 records falling between November and March. These are dry months in Region A & B, but are wet in Region C while in Region D October-November is the short rains. The climate in the breeding area is thus apparently unimportant, though more records are needed from Region C to show whether this kite breeds commonly south of the inter-tropical convergence zone at this season. In most places breeding peaks in November, and again in January-March; since this is the major peak (52/86 records) it probably represents a real maximum rather than relaying after earlier failure.

Scattered out of season records April-September are puzzling, but have been recorded both in recent times and by carlier observers (Jackson 1938). Some Black Kites are present in East Africa year round; conceivably these records, mainly from the Rift Valley in Region D and in Region B, may be by birds which have migrated north to breed from South Africa, at the opposite time of year to northern migrants. However, since southern M. m. parasitus are racially indistinguishable from northern birds, this suggestion is at present impossible to prove.

Being largely a true scavenger, this species may be able to obtain food at any time, and thus breeding may be unconnected with availability of food supply and be controlled more closely by climate and migration. Fuller data on this commonest of all large raptors are needed, especially from Region C.

Haliacetus vocifer African Fish Eagle M-P&G 160 Category (9) 275 records.

Region A. R. Nile II, 2; IV, 1; VI, 2; VII, 1;	
IX, 2; X, 3; XI, 3	14
L. Baringo V, 4; VI, 6; VII, 3; VIII, 1;	
IX, 4; X, 4	22
Region B. L. Victoria & W. Kenya. I, 2; IV,	
2; V, 6; VI, 1; VII, 2; VIII, 11; IX, 4;	
X, 2; XII, 3	33
W. Uganda I, 1; V, 1; VII, 1; VIII, 5;	
X, 4; XI, 2	14

Rwenzori Nat. Park. I, 2; III, 1; IV, 2;	
V, 1; VI, 4; VII, 14; VIII, 11; IX, 11;	
X, 13; XII, 2	61
Region C. II, 1; V, 2; VI, 1; VII, 2 .	6
Region D. L. Naivasha. I, 4; II, 12; III, 12;	
IV, 19; V, 17; VI, 17; VII, 9; VIII, 7;	
IX, 2; X, 1; XI, 6; XII, 4	111
Elsewhere. I, 1; II, 1; III, 1; IV, 1; V, 2;	
VI, 2; VII, 1; VIII, 1; X, 1	ΙI
Region E. V, 2; VII, I	3

There are enough records for the Fish Eagle to make an analysis worth while not only by regions but by individual populations, in particular rivers or lakes. Several systematic studies have been done (Brown 1960; Brown & Hopcraft 1973; Sumba unpub.) on Lake Victoria, Lake Naivasha, and in the Rwenzori National Park making it unlikely that the results from these areas are subject to bias derived from more random records. Many unpublished data available to L.H.B. have been used, and the literature adds a few records.

In Region A, results from the River Nile in Murchison (Kabalega) Falls National Park differ from those at Lake Baringo. They suggest breeding in almost any month with a possible increase at the end of the rains and early in the dry season. At Lake Baringo, however, there is a peak in May and June and another in November–December, both mainly dry seasons.

In Region B, on Lake Victoria, the season, with breeding in 9/12 months recorded, appears more elastic than it is in specific localities. In the Kavirondo Gulf near Kisumu, breeding is concentrated in July-December, occasionally January with a laying peak in August. Towards the Tanzanie border, however, records are for April-June, a season corresponding more with the few available records for Region C than with the Kavirondo Gulf 50-100 km north, on the same lake.

In western Uganda the season is elastic but there is a peak in July-October, a drier period between rains, both according to cards and a more systematic study (Sumba, unpub.).

The few records for Region C, mainly from Lake Victoria, bear out Stowell's (1958) statement that near Mwanza the Fish Eagle breeds May-October, wholly in the dry season; this agrees with the observed records from southwestern Kenya.

In Region D, the records from elsewhere are overshadowed by the large sample (111) from Lake Naivasha, where some breeding occurs in every month but there is a clear peak April–June—in and just after the main rains—with much laying also in February–March and an indication (after a minimum in September–October) of a secondary peak November–December, a wet season. Other records from Region D do not indicate any clear peaks but confirm that breeding occurs most of the year (9/12 months).

The few records for Region E, coastal, are for May, a wet month, and July, after the main rains.

Summarising, it appears that, in most of its range, the

Fish Eagle can breed equally well in dry or wet months, preferring sometimes dry seasons (Kavirondo Gulf, Tanzania Region C) and sometimes wet seasons (Naivasha). Available evidence makes it impossible to correlate these varying seasons with food supply, though the apparently fairly clear preference for dry season breeding on Lake Victoria in western Kenya and Tanzania suggests that climatic factors may override food supply in areas with long clear-cut dry and wet seasons. On the Kenya coast, where Fish Eagles occur year-round and apparently catch food with no difficulty, they seldom appear to breed. Better data from Lake Victoria, associated with the two main climatic regions on this lake (B & C) would be particularly useful in further studies.

Gypohierax angolensis Vulturine Fish Eagle or Palm Nut Vulture M-P&G 161 Category (5) 10? records.

Although the records are scanty, they indicate a clear laying peak July-August on Zanzibar and Pemba Island. Whether this is correlated with oil-palm fruit or some other factor remains to be established. The species is probably less dependent on oil palms in East than in West Africa.

Neophron percnopterus Egyptian Vulture M-P&G 110 Category (5) 8? records.

Region D. II, 1; III, 1?; V, 3; VI, 2; VII, 1 8? Scanty records indicate a peak of laying May-June, late in the long rains.

Gypaetus barbatus Lammergeier M-P&G 162 Category (5) 6 records.

In Region A the only record is for the dry season; in Region D most laying dates recorded (all but one in the same site) suggest most frequent laying the height of the long rains. At this site two possibly different females laid in January and in another nest in April–May. Although very many people have viewed this nest only a few have recorded even approximate dates.

Necrosyrtes monachus Hooded Vulture M-P&G III Category (7) 41 records.

In Region A this vulture lays late in and just after rains; in Region B in all (September-March) drier months with two June records from Toro, in a drier break in the rains. In Region D peaks are in and just after both rainy seasons. The single Region C record (close to Region D) is for November, a wet month.

Gyps africanus White-backed Vulture. M-P&G 107 Category (9) 115 records.

Region A. IV, 1; V, 2; VII, 1; XI, 1 . . 5
Region B. VII, 2 2
Region C. III, 13; IV, 35; V, 9; X, 1 . . 58
Region D. I, 9; II, 2; III, 1; IV, 6; V, 9; VI, 3; VII, 5; VIII, 4; IX, 5; XI, 1; XII, 6 . 50

Records are often difficult to date for egg-laying as nests are inaccessible and incubation and fledging periods long. Laying occurs in both wet and dry months in Regions A and D with a peak in Region D in the long rains, carrying on into the cool dry season and a second small peak in December after the short rains. In Region C there is a clear peak at the end of the rains in April.

In the single systematic study done (Houston 1976) in the Serengeti, laying peaks in March-May in the late rains-early dry season. Houston considered that this enabled recently fledged young to compete more effectively with adults for prey at the end of the dry season, when carrion was abundant, in September-October.

Gyps rueppellii Rüppell's Griffon Vulture M-P&G 106 Category (9) 165 records.

Region C. I, 48; II, 8; XII, 28 . . . 84 Region D. I, 6; III, 1; IV, 5; V, 4; VI, 26; VII, 3; VIII, 1; IX, 2; XI, 1; XII, 1 . . 81

In Region D laying is widespread, with a marked peak in June, and a smaller peak in January. Both North (1939) and Jackson (1938) (who wrongly identified the species as G. africanus) considered that most laying occurred in July or August. With a 55 day incubation period and a 110 day fledging period, young from eggs June-August would leave the nest in December-February.

Houston (1976) systematically studied this species in the Serengeti National Park, where it nests in the Gol Mountains, very close to the border of Region D, but forages mainly in Region C, up to 150 km from the nest sites. He considered that the laying date (December–January) may be triggered by rainfall but is geared to produce fledged young at the end of the dry season when carrion is most abundant, in June–July.

Good records are needed from northern Kenya, where this is by far the most abundant vulture. The only good dates are for August (Laisamis).

Aegypius tracheliotus Lappet-faced Vulture M-P&G 108 Category (8) 83 records.

This vulture lays in both wet and dry months, the scanty records for Regions A, B and D being almost equally divided, 6 dry, 7 wet. In Region C, where systematic studies were carried out by Pennycuick (1976), there is a clear peak April-July, late in and just after the rains with a

maximum in May, as dry weather begins. With a 55 day incubation period and a 110-120 day fledging period, young leave the nest in November-December, in the rains, when carrion is less abundant. However, this vulture may be less dependent on abundant large carcases than, e.g. Gyps spp.

Aegypius occipitalis White-headed Vulture M-P&G 109 Category (6) 19 records.

Most laying dates in Regions A, B and D (9/12) are in dry months. In Region C records indicate a laying season late in and just after rains, as in A. tracheliotus. This vulture is apparently the chief searcher (Kruuk 1967) and feeds on scraps dropped by other species; they depend on it, and it in turn on them.

Circaetus gallicus (incl. pectoralis and beaudouini) Blackbreasted and Beaudouin's Snake Eagle M-P&G 152, 154, 155 Category (4) 6? records.

The Region B record and all but one record in Region D are in dry months.

Circaetus cinereus Brown Snake Eagle M-P&G 153 Category (5) 9 records.

Region D. II, 1; III, 2; IV, 1; V, 1; VI, 1; VII, 2; VIII, 1

The few records indicate a widespread breeding season with no marked peaks.

Circaetus fasciolatus Southern Banded Snake Eagle M-P&G 156 Category (4) 2 records.

The two records are in the dry season after main rains. We reject a third record (Kreuger 1970) of a Category 1 at Ngong as doubtful because (a) the record is right outside the known range of *C. fasciolatus* (b) the habitat is quite unsuited to this species (c) the parent birds were apparently not positively identified, nor is the record substantiated by supporting data, as would be desirable for such an unusual record.

Terathopius ecaudatus Bateleur M-P&G 159 Category (7) 39 records.

The Bateleur breeds in both wet and dry months and has a widespread breeding season. 2/3 records for Region A are in wet months and those for Region B in a drier break between rains. In Region D, laying occurs in 9/12 months

with a peak (16/33 records) in February and March, the end of the hotter dry season, but there are eight records for May and December, late in the rains. The records do not indicate any close association with any particular food supply, but suggest that this scavenging, snake-and bird-eating species may prefer to breed when grass has been burned off. However, of the 39 records 21 are in months when the grass would be long if not green.

Polyboroides typus Harrier Hawk M-P&G 185 Category (6) 14 records.

Breeds in both wet and dry seasons, mainly wet; a fairly clear peak October–December (the short rains) in Region D continuing into the following dry season. This peak is *not* associated with maximum breeding among weaver birds, whose nestlings are apparently a favoured food.

Circus ranivorus African Marsh Harrier M-P&G 184 Category (4) 4 records.

All records are early in the cool dry season. Additional records are needed and should not be too difficult to obtain.

Melierax metabates Dark Chanting Goshawk M-P&G 180 Category (4) 4 records.

Region A. I, 1; VII, 1; X, 2 4

All records are in the dry season or at end of rains; more are needed to confirm data for this common species.

Melierax canorus Pale Chanting Goshawk M-P&G 179 Category (6) 17 records.

Region D. II, 3; III, 3; VIII, 2; IX, 3; X, 6 17

Breeds late in both dry seasons, with young in nest and fledging in the subsequent rains. Any connection with lizard abundance or availability is obscure. The food is not well known, but includes lizards, large insects and birds.

Melierax gabar Gabar Goshawk M-P&G 178 Category (5) 8 records.

This bird-eating species breeds at the same time as the supposedly lizard-eating *M. canorus*, late in the cool dry season, with young in the nest in the short rains, not a period of maximum numbers among resident passerines, though a season when Palaearctic migrants are abundant.

Accipiter melanoleucus Great Sparrowhawk M-P&G 174 Category (6) 14 records.

 Region A. IV, I
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Records from Region D indicate a definite peak April-

May, the height of the long rains; 5/8 are for one pair, but are confirmed by other records near Nairobi. This species feeds mainly on pigeons and doves (Brown in prep.), especially Streptopelia semitorquata and S. senegalensis. These show no very clear peaks of breeding in this region, but a slight peak May-July so that breeding by the sparrowhawk is not necessarily correlated with its favoured food supply, which is normally very abundant. It may conceivably be associated with altitudinal migration into the area by Olive Pigeons Columba arquatrix and Pinkbreasted Doves S. iugens, which are more abundant April-July than at other times of year. Olive Pigeons are taken by this hawk in greater numbers than their abundance would warrant. The Green Pigcon Treron australis is also taken more often than expected, especially late in the fledging period, although it should be most abundant December-March when this hawk is not breeding.

Accipiter ovampensis Ovampo Sparrowhawk M-P&G 172 Category (4) 2 records.

This species is apparently mainly a migrant to Kenya from further south, breeding only sporadically; the records are for the cold season further south and neither were known to succeed, one clutch being taken and another failing to hatch (Brown 1970b).

Accipiter rufiventris Rufous-bellied Sparrowhawk M-P&G 173 Category (3).

No definite records, but observations at Mau Narok suggest breeding November-December, after the main rains.

Accipiter minullus Little Sparrowhawk M-P&G 170 Category (4) 5 records.

Scanty records suggest a peak in October, early in the short rains.

Accipiter tachiro African Goshawk M-P&G 177 Category (7) 25 records.

Apparently lays in both wet and dry months with a peak March-May (long rains) and a greater peak October-November (short rains) in Region D. Thus this species lays in both rains and could be expected to take advantage of a post-rains peak of abundance of small birds. However, its food also includes mammals, and the indications of a major peak in the short rains (11/23 Region D records) does not accord with the period of maximum breeding

among Passerines, which is the long, not the short rains.

Accipiter badius Shikra M-P&G 176 Category (4) 4 records.

An unaccountably scarce species in East Africa in suitable habitat. The two records for Region B are in the dry season, but those for Regions A and D are in months of high rainfall.

Kaupifalco monogrammicus Lizard Buzzard M-P&G 150 Category (5) 9+ records.

The records are no better than indicative in any region, but suggest breeding late in both dry seasons in Region D, and mainly in dry months elsewhere.

Buteo oreophilus Mountain Buzzard M-P&G 165 Category (4) 4 records.

All the scanty records indicate that this species of highrainfall forests lays in the dry seasons; however, its period of maximum food demand would then fall in the rains.

Buteo rufofuscus Augur Buzzard M-P&G 167 Category (8) 75 records.

Records for Regions B and D, with two rainy seasons and two dry seasons more or less clearly separated, indicate an extended breeding season (1 record in each of 7 months in Region B) with a peak (33/55 records) in the cool dry season June-September in Region D and a probable secondary peak in February and March (10 of the remaining 22 records). Laying in the dry season would normally mean peak food demand with large young in the nest about two months later, usually in the rains, when cover is long and the 10dents which are the preferred food of this buzzard may be more difficult to catch. The available data for Region D thus do not accord well with theoretical conclusions on the availability of food at the time of maximum demand for young in the nest.

At high altitudes (Mt Elgon, Mt Kenya) the few available records suggest that this buzzard breeds in the main dry season, climatic conditions probably overriding food supply as the proximate factor controlling laying date.

Aquila rapax Tawny Eagle M-P&G 139 Category (7) 44 records.

Records from Region D indicate an extended breeding season beginning just before or early in the long rains, peaking in May-July, and thereafter declining; eggs are laid both in wet (12/36) and predominantly dry (24/36) months, but the average of two wet months (6) is higher than in seven dry months (mean 4). This species has a varied diet including carrion, and this extended breeding season may take some advantage of peaks of game bird numbers. In Region A records indicate peak laying late in the rains and early in the long dry season. Records for Region C are inadequate, one being in a wct and one in a dry month. Migrant Steppe Eagles A. r. orientalis are present in Region A when resident A. r. rapax are breeding, but not in Region D; this evidently makes no difference to successful breeding as the Region A pattern applies also in Ethiopia where A. r. orientalis is more abundant October-March than in East Africa.

Aquila wahlbergi Wahlberg's Eagle M-P&G 142 Category (8) 91 records.

 Region A. VIII, 1; IX, 1
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 Region B. VIII, 1; IX, 8; X, 1
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 Region C. IX, 1
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Wahlberg's Eagle migrates south into East Africa in August, and lays mainly in September-October regardless of the rainfall pattern. Its breeding dates are apparently controlled by its migratory habit, as in the Black Kite. We have rejected one record for June, of an egg probably laid May, for Kondoa Irangi as it would be completely out of pattern, and could be due to misidentification, although it derives from a normally very accurate observer (J. S. S. Beesley). There is some suggestion that in Regions A and B, nearer the equator, breeding may peak in September rather than October somewhat further south. There is no connection between the breeding peak and more abundant food supply in this species.

Aquila verreauxi Verreaux's Eagle M-P&G 136 Category (7) 34 records.

Records for Region A are all from Baringo district and those for Region C all from Serengeti, in the hottest dry season and early in the dry season respectively. In Region D breeding begins in the main rains and peaks in the cool dry season June–July. However, records for some sites in the Rift Valley in this region are mainly for April and May. There is no obvious connection between abundance

of food supply (98% Rock Hyrax in this species) and breeding seasons.

Hieraactus spilogaster African Hawk Eagle M-P&G 143 Category (7) 35 records.

In Region A records indicate breeding early in the dry season, and in Region B the few records suggest extended breeding. In Region D breeding begins late in the long rains with a very definite peak in Junc-July; this corresponds with maximum numbers of game birds (guineafowl, francolins) and a cool season, so that in this species the correlation between breeding season and food supply is good.

Hicraaetus dubius Ayres' Hawk Eagle M-P&G 144 Category (7) 30 records.

Apart from one in Region A (Londiani) all records are from two sites in Embu District, observed for 28 and 9 years continuously. Records from the first site include two replacement clutches after carlier failure, in September and March. Peak laying is from late May-August (18/29 records) but, within this period, appears to depend on the idiosyncrasies of individual females as much as anything else, some consistently laying May-June, others late July-August. Although this species feeds on very abundant small birds and doves, it is a very irregular breeder, one pair having laid only three times from 1965-76 (12 years) the last two eggs by the same female in August 1974 and 1976. Reasons for this apparently poor breeding record have been discussed by Brown (1975). Accepting that Junc-August is the peak laying season, the maximum food demand occurs late September-November, which does not coincide with maximum numbers of small birds though at that time reduced leaf cover could make them easier to catch.

Lophactus occipitatis Long-crested Eagle M-P&G 149 Category (7) 29 records.

This largely rodent-eating forest edge and woodland species has an elastic breeding season, but most records are for dry or predominantly dry months (13/14 in Regions A. B and C). In Region D, 10/14 records are for dry months and in Region E the only record is after the main rains.

However, records from Region D indicate that laying in the same site can occur in March (dry) and November (wet) suggesting that breeding may be opportunistic at times: years apparently pass without breeding in the same area.

Stephanoaetus coronatus Crowned Eagle M-P&G 147 Category (7) 42? records.

Most records come from Embu District (Region D) where one site has been recorded for 28 consecutive years, and in Region A from Mau Narok. The Region B records are for one intermittently observed nest in Bwamba Forest, and apart from a doubtful June record, are for December-January (dry). In Region A laying occurs mainly September-January, late in or just after the rains, but within this period actual dates depend on individual females. In Region D there is a peak June-October, laying in the cool dry season; again, individual females may prefer to lay in certain months but at one nest (Karen: Brown 1966), the same female laid on dates varying from end Juneearly December. This eagle has a very protracted postfledging period of 9-11 months in Kenya, and if this or another stage of the breeding cycle is terminated prematurely by accident or disaster a new cycle may start at an unusual date. Thus one November, Region D, record is a re-laying, following a June failure, and the other November and single December record both follow premature deaths of flying young. Thus, although there appear to be peak laying periods, in wet and dry months respectively, in Regions A and D, breeding at an unusual time can be triggered by failure at some stage of the 20-22 month cycle, and there is no clear connection between season, food supply, and peak laying dates.

Polemaetus bellicosus Martial Eagle M-P&G 146 Category (7) 48 records.

Records are only adequate for analysis from Region D, where one site has been recorded for 28 years, others for 4-8 years in succession. These indicate a clear peak in and just after the long rains, April-May, and a probable secondary peak in August (cool, dry). However, the second peak is affected by the behaviour of individual females, and late laying may sometimes be associated with building a new nest. However, the few records for Regions A, C and E are also in or late in the rains. This eagle feeds largely on game birds and poultry and a peak laying season April-August could accord with maximum abundance of game birds late in the cool dry season, about August-

September. Unlike *Stephanoaetus coronatus* this species has no prolonged post-fledging period and can breed annually.

Sagittariidae Secretary Bird

Sagittarius serpentarius Secretary Bird M-P&G 103 Category (7) 45 records.

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Region A. III, 1; IV, 1; V, 1; IX, 1; X, 1 . 5
Region C. I, 1; VII, 1; VIII, 1; XII, 1 . 4
Region D. I, 2; II, 3; III, 3; IV, 1; V, 7; VI, 3; VII, 1; VIII, 2; X, 4; XI, 5; XII, 5 . 36
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Region D records indicate a widespread breeding season with two peaks late in and just after the long rains (10 records May-June) and again in the short rains (14 records October-December). These are both periods when the grass is long and lush and large insects are abundant. However, large young would be in the nest some three months after these dates, at the height of the dry seasons, in August-September and January-March; this could coincide with grass burning, killing insects and exposing rodents and reptiles to predation. The scanty records for Regions A and C indicate laying both in rains and dry seasons.

Falconidae Falcons

Polihierax semitorquatus Pygmy Falcon M-P&G 129 Category (4) 2 records.

Region D. IX, 1; XII, 1 2
Both records are in dry seasons.

Falco rupicoloides White-eyed or Greater Kestrel M-P&G 124 Category (6) 14 records.

Region C records are for late in the rains and early dry season; in Region D eggs are laid in 7/12 months with a probable peak in and just after the main rains, confirming the tendency in Region C. Laying and rearing young would coincide with long unburned grass in most cases.

Falco alopex Fox Kestrel M-P&G 125 Category (4) or (5) 20+ records.

Falco timunculus Kestrel M-P&G 123 Category (4) 5 records.

The scanty records indicate laying late in the rains or in dry seasons. This species is unaccountably scarce as a breeding bird in Kenya in apparently ideal habitat.

Falco ardosiaceus Grey Kestrel M-P&G 127 Category (4) 2? records.

The single definite record (Loosemore 1963) indicates laying in September. Two more recent records on cards, too indefinite to date accurately, but of flying broods also suggest laying September-October. Indications are that this species breeds in the dry season, apart from the April record in Mackworth-Praed & Grant (1957) which does not give source details.

Falco dickinsoni Dickinson's Kestrel M-P&G 128 Category (3).

The only records are for Pemba (Region D, coastal) which suggest laying July-October (Pakenham 1943).

Falco chicquera Red-necked Falcon M-P&G 122 Category (4) 2 records.

Region E. VII, 1; VIII, 1 2

The two records are for broods of three in Borassus palms near Garsen and Ukunda in the dry season.

Falco cuvieri African Hobby M-P&G 116 Category (5) 10 records.

Five records from Region B indicate most breeding in the dry season December–March but 3/5 others are for the rains. This insectivorous species might be expected to breed in the rains but feeds its young on small birds (Forbes-Watson 1963).

Falco biarmicus Lanner Falcon M-P&G 113 Category (4) 5 records.

Region D. VI, 3; XII, 2 5

The scanty records suggest laying early in either of two dry seasons. As this is by far the most common of the large falcons in East Africa, more records from several regions should be easy to obtain.

Falco peregrinus Peregrine Falcon M-P&G 112 Category (5) 14 records.

Region D. VI, 1; VII, 1; VIII, 11; IX, 1 . 14

A very definite peak in August, late in the cool dry season. The time of maximum food demand for large young in October coincides with the arrival of numbers of migrants from the Palaearctic; amongst other birds this falcon feeds on European Bee-eaters Merops apiaster. However, further study of food preferences would be needed before any definite correlation between the Peregrine's breeding season and the arrival of Palaearctic migrants could be established. Eleonora's Falcon F. eleonorac, the Sooty Falcon F. concolor, and the Lanner F. biarmicus are all known to depend partly or wholly on Palaearctic migrants for successful breeding.

Phasianidae Game birds

Francolinus lathami Forest Francolin M-P&G 189 Category (4) 1 record.

Young about one month old have been shot in September (van Someren 1914, 1916) and females with enlarged gonads collected May and June, suggesting breeding late in or just after the main rains.

Francolinus naham Nahan's Forest Francolin M-P&G 190 Category (4) 1 record.

Francolinus coqui Coqui Francolin M-P&G 161 Category (7) 23 records.

Most records are for the rains or early dry season following, when grass is long and unburned.

Francolinus streptophorus Ring-necked Francolin M-P&G 193 Category (3).

Stated by Jackson (1938) to breed in western Kenya, Region B December-March and in northern Uganda (Gulu and Chua Districts) in April; i.e. in the dry season in Region B andearly rains in Region A. No recent records at all.

Francolinus sephaena Crested Francolin M-P&G 194-195 Category (7) 37 records.

In Region A the scanty records are for dry months and in Region B in the drier break after main rains. All but one Region C record are in rains, and in Region D breeding occurs in most months but with a peak in the main rains (8/20 records April-May). Laying in Region E is apparently concentrated after the main rains. There is no clear correlation between climate and laying date in this species.

Francotinus shelleyi Shelley's Francolin M-P&G 196-198 Category (5) 8 records.

Identification of this francolin is often confused; indications are that it breeds in dry seasons, in both Region C and D.

Francolinus psilolaemus Montane Red-winged Francolin M-P&G 198 Category (5) 10 records.

 All records are from Mau Narok (P.H.B. Sessions) and indicate widespread breeding but mainly in the first half of the year, peaking in the rains.

Francolinus levaillanti Red-winged Francolin M-P&G 199 Category (7) 20 records.

In Regions A and C this species apparently lays mainly in the rains but in Region B fuller records indicate a peak at the beginning of the dry season after the main rains, when grass is longest and unburned.

Francolinus hildebrandti Hildebrandt's Francolin M-P&G 203 Category (7) 26 records.

Breeding is concentrated in dry months or at end of rains (23/26 records) but it may occasionally breed also in the rains. Records of uncertain age from Narok District (Betts 1966) state many pairs with half grown chicks in June, indicating breeding late in the rains or early dry season.

Francolinus icterorhynchus Heuglin's Francolin M-P&G 201 Category (5) 6 records.

The scanty records indicate breeding either in rains or dry season, preferring rains.

Francolinus afer Red-necked Spurfowl M-P&G 208 Category (7) 47 records.

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Region B. I, 12; II, 1; III, 1; IV, 2; V, 1;
VII, 2; IX, 1; X, 2; XI, 1; XII, 10 . 33
Region C. II, 1; III, 3; IV, 2; VII, 1 . 7
Region D. V, 1; VI, 2; VII, 1; XII, 1 . 5
Region E. VI, 2 . . . . . . . 2
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Region B records are biased by one card with 20+records, but indicate a widespread breeding season with no obvious peaks other than those in December-January resulting from that one card. In Regions C, D and E breeding occurs late in and just after rains (both seasons, Region D) when grass is long and lush.

Francolinus rufopictus Grey-breasted Spurfowl M-P&G 209 Category (5) 10 records.

Region C. II, 3; III, 1; IV, 1; VI, 2; VII, 3. 10 Breeds in wet and dry seasons, possibly preferring dry.

Francolinus leucoscepus Yellow-necked Spurfowl M-P&G 210 Category (8) 52 records.

Region D records indicate some breeding in most months but a peak May-July (22/44 records) in and just after the main rains and some indication of a secondary peak in the short rains; however, breeding varies according to the rains in any year. Region C records are from Tarangire, close to Region D, late in the rains.

Francolinus jacksoni Jackson's Francolin M-P&G 206 Category (6) 14 records.

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Region A. I, 1; II, 1; VIII, 1; X, 1; XII, 1 5
Region D. I, 3; VII, 1; XII, 5 . . . . 9
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Region D records indicate a definite peak in the driest season December-January with a single exception from Kijabe (in the Rift Valley) also in a dry month. Region A records are more widespread but are also mainly in dry months. At high altitudes such species may only be able to breed in the driest months.

Francolinus squamatus Scaly Francolin M-P&G 204 Category (7) 38 records.

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Region A. I, I; III, I; V, I; XII, 2 . . . 5
Region B. I, I; II, I; III, I; V, I; VI, I;
VII, I; X, I; XI, I . . . . . . 8
Region D. I, 3; IV, I; V, I; VI, 3; VII, I;
VIII, 4; IX, 10; XI, I; XII, I . . . 25
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All records indicate a widespread breeding season (with one record in each of 8/12 months in Region B). In Region D eggs are laid in 9/12 months but there is a peak in August–September (14/25 records), the end of the cool dry season. There may be subsidiary peaks late in both rains, May and January. This forest species has rather less definite breeding seasons than most francolins, but prefers drier months.

Coturnix coturnix Quail M-P&G 211 Category (7) 35 records.

Most records are from the high plateaux on either side of the Rift Valley in Kenya, with rather similar ecology but different rainfall regimes. In Region A (Mau Narok) the season is widespread with a peak in December (dry) and another in July-August (wet). In Region D most records are for the driest months January-March on the Kinangop (11/17). No very clear connection with climate emerges from this, but dry months are preferred in these rather cold wet areas.

Coturnix delegorguei Harlequin Quail M-P&G 212 Category (7) 23+ records.

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Region A. I-II many; VIII, I . . . I+
Region C. IV, I; VI, I . . . . 2+
Region D. IV, 2+, V, 6+; VI, 4; VII, I;
XI, 5; XII, 2 . . . . . 20+
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Records are not representative of the total numbers breeding in any locality, as this nomadic species appears to settle and breed in large numbers locally where conditions are temporarily suitable. Thus Jackson (1926) found 'many nests wherever the grass is short' on the Turkwell River in January and February (dry) and 'great numbers' between Yonte and Afmadu in Jubaland in November (wet). A recent card from Kisima (near Nanyuki, Kenya) states that the species was incredibly abundant 1-25 November 1975, immediately after good rains. Likewise in Meru National Park in 1972 a few definite records cover only a small fraction of the breeding pairs present. The Region D records do in fact indicate peaks in and after both rainy seasons; but such peaks are very irregular and these quails do not breed regularly in the same areas at the same season. They are nomadic and opportunistic breeders, nesting in numbers when they can, apparently after locally good rains.

Coturnix chinensis Blue Quail M-P&G 213 Category (5) 7 records.

Region A. VII, 1		1
Region B. V, 1; VI, 3; VII, 1		5
Region D. VIII, 1		1

The records are too few to be much more than indicative, but in Region B suggest a peak late in the long rains, and in A and D also after the main rains in a drier break.

Ptilopachus petrosus Stone Partridge M-P&G 214 Category (4) 1 record.

Region A. XII, I I

The single record is for the dry season.

Numididae Guineafowls

Numida meleagris Helmeted Guineafowl M-P&G 215, 216 Category (8) 55 records.

Despite its abundance and familiarity, good definite dated records of eggs or young that can be aged are scarce. Widespread breeding is indicated in all regions but mainly in and after the first rains in Region A, perhaps also in Regions B and C. In Region D laying is recorded in 10/12 months but with a peak May–July just after the long rains and a second peak in December, late in the short rains. Guineafowl prefer to breed when the grass is long.

General observations indicate that guineafowl flocks immediately break up into pairs with the onset of good rains, at least in drier areas, and aggregate into larger flocks with their broods at the end of the rains. Non-breeders may remain in flocks during the rains, and pairs do not always persist in breeding if rains do not continue.

Guttera edouardi Crested Guineafowl M-P&G 217 Category (6) 13 records.

Seven out of 13 records are for dry and 6 for wet months; indications are of a widespread breeding season with no pronounced peaks but more data are needed.

Guttera pucherani Kenya Crested Guineafowl M-P&G 218 Category (4) 6 records.

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Region E. IV, 2; VI, 1; VII, 1; VIII, 1; XII, 1 . . . . . . . . . . . . . . . . .
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The few definite records indicate a prolonged breeding season. Mackworth-Praed & Grant (1957) give April-June, and in Zanzibar (Region D) April onwards. More data are needed before any conclusions can be drawn.

Acryllium vulturinum Vulturine Guineafowl M-P&G 219 Category (6) 14 records.

This species of semi-arid thornbush probably breeds in or just after either rainy season, with a peak in June and a second peak December-January. The statements of Jackson (1938) repeated by Mackworth-Praed & Grant (1957) to the effect that it breeds in Tsavo February-April (dry season and early rains) are erroneous on the basis of the available good dated records.

Turnicidae Button Quails

Turnix sylvatica Button Quail M-P&G 365 Category (6) 19 records.

The surprising number of good dated records for this secretive species show that in all regions it breeds mainly in or just after the rains (in both rainy seasons, Region D), occasionally in normally dry months (3/19 records).

Turnix nana Black-rumped Button Quail M-P&G 366 Category (5) 10 records.

The records indicate a clear peak June-July in Region A, when the main rains have begun; occasional records for Region A and B are at the end of the rains. Mackworth-Praed & Grant (1957) also give July and November for Region B, without precise details.

Ortyxelos meiffrenii Quail Plover M-P&G 367 Category (3).

Said by Mackworth-Praed & Grant (1957) to breed in northern Kenya in December and January, after the short rains: source unknown.

Gruidae Cranes

Balearica pavonina Crowned Crane M-P&G 244-245 Category (8) 99 records.

The good sources of cards and other records for this species indicate a clear preference for breeding in the rains in Region A (7/10 records) and Region C (12/13 records). In Regions B and D where the seasons are less clear-cut breeding may occur in almost any month (12/12 Regions B and D); but in Region B, with high rainfall there is a peak in the dry season November-March (20/34 records) and in Region D, in relatively low rainfall with more distinct seasons, a peak in the long rains continuing into the cool dry season April-July (33/42 records). In most areas there is a preference for breeding in the rains, but in the wettest parts of East Africa the dry season is preferred.

The situation is more complicated than this, however, as in some perennial swamps a fiesh breeding cycle is apparently initiated by the loss of a clutch or a dependent juvenile (Sessions 1967 and cards; Turner, cards). This type of behaviour could account for continued dry season breeding in reduced numbers following a rainy season peak, but scarcely for the dry season peak in Region B. Food supply in perennial swamps is probably always adequate and breeding is apparently triggered by climatic conditions, and repeated without delay if the attempt fails; further detailed observations on this would be valuable.

Rallidae Rails, Crakes, Coots, Gallinules

Rallus caerulescens African Water Rail M-P&G 222
Category (3)

Mackworth-Praed & Grant (1957) state that this rail is recorded breeding in Kenya in June, with no details.

Crex egregia African Crake M-P&G 224 Category (5) 9 records.

All records indicate that the African Crake breeds in or late in the main rains.

Porzana marginalis Striped Crake M-P&G 226 Category (4), 1 record.

Region D. VI, r r

Late in the main rains, cf. Crex egregia. On the basis of gonad activity Pitman (1965) considered that it would breed in Region C (Tabora) January, and Region D May and June (all in rains).

Porzana pusilla Baillon's or Lesser Spotted Crake M-P&G 228 Category (3).

Friedmann & Loveridge (1937) collected a bird at Kilosa, Region D with enlarged ova, suggesting breeding in the rains.

Limnocorax flavirostra Black Crake M-P&G 225 Category (8) 87 records.

Where records are adequate (Regions B and D) they indicate a widespread breeding season with peaks in and just after main rainy seasons. The Region B records may be to some extent biased by specific collecting expeditions by C. R. S. Pitman, but this is probably unimportant. Regions A, C and E records tend to confirm that breeding reaches a peak in or just after the main rains but are inadequate for any detailed analysis.

Sarothrura rufa Red-chested Crake M-P&G 233 Category (4) 2 records.

Sarothrura boehmi Böhm's Crake M-P&G 231 Category (3).

Possibly VI Region B; VII Region A.

Sarothrura elegans Buff-spotted Crake M-P&G 236 Category (3).

Possibly IX Regions A and B; VII Region D (Pemba).

Sarothrura pulchra White-spotted Crake M-P&G 235 Category (3).

Possibly II, IV, IX in Region B.

Sarothrura affinis Chestnut-tailed Crake M-P&G 230 Category (4) 1 record.

Region A. V, r r

Region C possibly I; Region D possibly III.

The data available for Sarothrura spp. are no better than indicative for any species. The rare dated records suggest breeding in the dry season (S. rufa Region D) or in the wet season (S. affinis Region A). The data have been summarised by Keith et al. (1970) who conclude that a record formerly accepted for S. boehmi actually applies to S. affinis.

Gallinula angulata Lesser Moorhen M-P&G 240 Category (5) 10 records.

All the scanty records except two in March in Region **D** are for wet months or after the main rains.

Gallinula chloropus Moorhen M-P&G 239 Category (7) 46 records.

There appears to be a pronounced peak in breeding in Region B in June, late in the main rains, perhaps in a somewhat drier break. Region C records are all for wet months, but in Region D (mainly at Lake Naivasha) breeding occurs in 11/12 months with a pronounced peak in June, perhaps biased by 8 recent records from the Rift Valley, without which no pronounced peaks would appear. There are more records for the cool dry season June-September, 20/33, than for the remaining eight months of the year.

Porphyrio porphyrio Purple Gallinule M-P&G 237 Category (6) 12 records.

Available records suggest a preference for breeding in or late in rainy seasons. This species disperses to temporary ponds, e.g. in Embu District (where it may breed) in seasons of unusually heavy rains.

Porphyrio alleni Allen's Gallinule M-P&G 238 Category (5) 6 records.

The few records indicate a preference for breeding in dry months following the long rains cf. Gallinula chloropus.

Fulica cristata Red-knobbed Coot M-P&G 242 Category (8) 84 records.

Where records are adequate (Regions A and D) they indicate widespread breeding, in all months in Region D. However, in this region there is a clear peak May-July (26/49 records) after the main rains and a secondary peak in the late dry season September-October (10 of the remaining 23 records). In Region B a peak is suggested in the main rains, April, but could be biased by a few collecting trips by C. R. S. Pitman. Region A records (mainly Mau Narok) suggest a peak in September, late in the main rains, thus tending to support the Region D findings. Unfortunately, when 'many' nests have been found (Thomas 1960; van Someren, cards) they are not counted or properly recorded so that quite possibly real peaks of breeding are obscured, as those records of 'many' nests do not always agree with peaks as brought out above.

Better and more careful records of peak breeding times on this most abundant and obvious of all Rallidae are needed.

Heliornithidae Finfoots

Podica senegalensis African Finfoot M-P&G 243 Category (4) 2? records.

The single dated record is for two eggs near Lunga Lunga, southeastern Kenya after the main rains. The only record for Region D is of a half-grown chick on 1 October 1977, suggesting hatching late August from eggs laid perhaps July.

Otididae Bustards

Otis kori Kori Bustard M-P&G 250 Category (6) 18 records.

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Region A. I, I . . . . . . . . I
Region C. II, 4; III, 3; IV, 2 . . . 9
Region D. I, 1; II, 2; III, 1; IV, 2; VI, 1;
XI, I . . . . . . . . . . 8
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Seasonal preference is conflicting; in Region C there is an apparent peak towards the end of the rains but elsewhere dry months are preferred.

Neotis denhami Denham's Bustard (including Jackson's Bustard) M-P&G 251 Category (7) 9(+12) 21 records,

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Region A. I, 4; II, 1; III, 2 . . . 7+ 12
Region C. III, 1; VII, 1 . . . . 2
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In Region A a clear peak in the late dry season is confirmed by 12 not precisely dated records from Pitman for Acholi and northeastern Karamoja from 12 December-3 March; the two records for Region C are in the late rains and dry season. This species clearly prefers to breed in the driest months. There are no definite records for Kenya but Mackworth-Praed & Grant (1957) mention March-June and November, which could be wet or dry according to locality (unspecified).

Eupodotis ruficrista Buff-crested Bustard M-P&G 257 Category (4) 2 records.

Scanty dated records are for both wet and dry months. However, Jackson (1938) and Mackworth-Praed & Grant (1957) give breeding in Kenya March-June (rains) and August (dry). More data are needed.

Eupodotis senegalensis White-bellied Bustard M-P&G 256 Category (5) 7 records.

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Region C. I, 1; II, 1; IV, 1; V, 1; XII, 1 . 5
Region D. V, 1; X-XI, 1 . . . . . 2
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All dated records are for the rains. However, both Jackson (1938) and Mackworth-Praed & Grant (1957) mention February, a dry month.

Eupodotis melanogaster Black-bellied Bustard M-P&G 258 Category (6) 18 records.

In Regions A and B this bustard lays at the end of the dry season extending sometimes into the rains; in Region C there are records for wet and dry months. Mackworth-Praed & Grant (1957) state that it breeds in coastal areas (Region E) in March-April, also October (wet and dry). Indications are that it prefers the late dry season where this is clearly defined.

Eupodotis hartlaubii Hartlaub's Bustard M-P&G 259 Category (4) 3 records.

Iacanidae Jacanas

Actophilornis africana African Jacana M-P&G 264 Category (8) 71 records.

Records from Region A indicate a preference for breeding in the rains but 4/II are in the dry season. Elsewhere, breeding appears to peak late in, or just after rains, in both seasons in Region D May-July and December-February with 17/37 and 11/37 records respectively. Breeding is thus widespread but tends to peak at a season when the floating nests and eggs may be less likely to be swamped and chilled.

The single definite dated record is for the rains. However, Mackworth-Praed & Grant (1957) give February-May for Kenya, dates indefinite.

Rostratulidae Painted Snipes

Rostratula benghalensis Painted Snipe M-P&G 297 Category (5) 9 records.

In both regions nests chiefly after the heaviest rain. Anon. (1950) also mentions many nests at Kinyampidzi, Lake Edward, in June and Mackworth-Praed & Grant (1957) state that it breeds in Uganda June-July and in Kenya August, September and other times. Some of these vague dates agree with our dated records.

Charadriidae Plovers

Vanellus crassirostris Long-toed Plover M-P&G 293
Category (6) 17 records.

 The Long-toed Plover breeds in Region B either in the dry season or in the drier break after the heaviest rain, peaking in June. Records elsewhere are for dry months.

Vanellus armatus Blacksmith Plover M-P&G 287 Category (9) 115 records.

Good records for Region D demonstrate that peak breeding occurs just after the long rains and in the cool dry season with 80/103 records May–July. This tendency is confirmed in Region C where the figures indicate a peak May–June, early in the dry season.

Vanellus spinosus Spur-winged Plover M-P&G 286 Category (9) 106 records.

Region A records, mainly from northern Uganda, indicate a clear laying peak in the main rains in April; rather numerous records for February-March could be a response to early rains. A peak in laying in the rains is confirmed by the Region D records, mainly from Lake Turkana, and the few records from Region B.

Vanellus tectus Black-headed Plover M-P&G 292 Category (7) 36 records.

In Region D there is a clear peak at the height of the main rains, continuing to some extent through the subsequent dry season. Region A records are, in contrast (6/9), mainly for dry months. At present it appears that this plover might adapt its laying season according to particular rainfall conditions, as with some other *Vanellus* spp.

Vanellus albiceps White-headed Plover M-P&G 290 Category (5) 9 records.

Region C. VII, 1; VIII, 1; IX, 6; X, 1 . 9
Although the records are few they indicate a clear peak of breeding in September, the end of the dry season, when river flows are lowest and sandbanks exposed.

Vanellus lugubris Senegal Plover M-P&G 282 Category (7) 23 records.

The records are inadequate for satisfactory analysis in any region but indicate a preference for dry season breeding in Regions B, C and D. This may prove to be another plover (cf. *V. tectus*) which may vary its breeding season according to the rains in particular areas.

Vanellus melanopterus Black-winged Plover M-P&G 283 Category (8) 63 records.

The good records for Region D indicate a very clear peak at the end of the hot dry season February-March (34/46 records). Peak laying in March probably corresponds to short green grass following 'grass rains'. In Region A laying is for April-June in the main rains and for Region C most records are for the dry season, but scanty. The Region A records are mainly from Mau Narok and Trans Nzoia, and in fact are for early rains before the ground is really wet.

Vanellus coronatus Crowned Plover M-P&G 281 Category (9) 174+ records.

Records for Region C indicate a clear dry season peak (51/71 records May-September) with more nests in September than indicated ('many', Thomas 1960). In Region D, however, the peak occurs in and just after the main rains (50/99 records April-June, with another 10 in March and 11 in October, probably after early rain). Region D is generally rather drier than Region C, so that optimum breeding conditions may occur there at quite a different season to Region C. Better records from Serengeti would be valuable in this connection.

Vanellus senegallus Wattled Plover M-P&G 291 Category (7) 35 records.

Region A records indicate a clear peak March-April, some also February and May (18/21 records) laying late in the dry season and into the early rains. In Region C, however, there is a clear dry season peak August-October with a few early rains records. The Region B records are all for the mid-rainy season peak July-September.

Charadrius pecuarius Kittlitz' Sand Plover M-P&G 271 Category (9) 160 records.

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Region A. I, 2; II, 3; III, 2; IV, 4; V, 7;
VI, 5; VII, 5; VIII, 1; XII, 1 . . . 30
Region B. IV, 2; V, 1; VI, 8; VII, 8; VIII, 3;
IX, 1 . . . . . . . . . . . 23
Region C. II, 1; IV, 2; V, 1; VI, 9; VII, 1;
IX, 4 . . . . . . . . . . . . . . . 18
Region D. I, 3; II, 5; III, 3; IV, 5; V, 18;
VI, 8; VII, 14; VIII, 9; IX, 9; X, 1; XI, 5; XII, 9 . . . . . . . . . 89
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Records are adequate for a good assessment in all four regions. In Region A peak laying is from April-July (21/30 records) the height of or just after the main rains. In Region B, in contrast, most breeding occurs June-August (19/23 records) and more indefinite records (many nests: Anon. 1950) confirm that the peak laying is after the long rains and in the mid-year drier break. In Region C peak laying is June-September, the dry season (cf. Region A, where the peak is near the height of the wet season). In Region D peak laying is in the long rains April-May (23/89 records) continuing through the cool dry season June-September (40/89 records) with a secondary peak in the short rains November-December (14/89 records). Thus this little plover tends to prefer breeding in the rains or in the mid-year drier or dry season except in Region C where records indicate a surprisingly strong preference for breeding in the dry season. This result may be biased by Reynolds, (1968) records, mainly obtained in areas which were flooded during the rainy season.

Charadrius tricollaris Three-banded Plover M-P&G 272 Category (8) 53 records.

Records are inadequate for Regions A, B and E, but in B indicate a preference for rains breeding, which confirms those for Region D where the peak is April–July with a secondary small peak in December, in the short rains. In Region D this plover tends to breed just after the height of the rains. In Region C, however, 9/11 records are for the dry season, with a peak June–July, soon after the rains. At least locally (along the Ruaha River) this plover depends on exposure of river sandbanks, like the African Skimmer and Water Thicknee (Reynolds: pers comm).

Charadrius marginatus White-fronted Sandplover M-P&G 268 Category (5) 7 records.

All Region D records are coastal but one; perhaps the two regions should be combined in this species. Breeding occurs mainly just after the long rains.

Charadrius pallidus Chestnut-banded Sandplover M-P&G 270 Category (9) 130 records.

A very clear peak late in and after the long rains up to July; figures for some months may be biased by large numbers of clutches found in a single day; however, the pattern seems clear enough. In Region C probably a similar pattern will emerge with more records.

Scolopacidae Sandpipers, Snipes

Actitis hypoleucos Common Sandpiper M-P&G 312 Category (4) 1? record.

This is the contested record for the Common Sandpiper discussed by Benson & Irwin (1974). The actual extract from R.A.L. & V.G.L. van Someren's record book (extracted for us by G. R. Cunningham-van Someren) reads "Totanus hypoleucos. Buddu. Eggs/young, June.", a bare statement without any supporting data, despite the obvious extraordinary interest of this record.

Since there have never been any further indications that this species breeds in East Africa we consider that this record can at best be accepted with great reserve; Benson & Irwin (1974) accepted it, though equally with reserve.

Gallinago nigripennis African Snipe M-P&G 300 Category (7) 21 records.

All indications are that this snipe breeds in the main rainy season or just after, occasionally in the dry season (November Region B). Most records are exactly dated clutches of eggs; no recent records at all.

Recurvirostridae Avocets and Stilts

Himantopus himantopus Black-winged Stilt M-P&G 296 Category (7) 45+ records.

Breeds in Region D mainly late in the long rains and the cool dry season and in Region B in and after the long rains.

Recurvirostra avosetta Avocet M-P&G 295 Category (8) 72 records.

Avocets breed only on certain alkaline lakes, notably Lake Magadi, where most records originate. Here they begin breeding in the long rains and peak June–July, early in the cool dry season. Rarely, breeding also occurs after the short rains, in February. Region C records indicate

a similar pattern of laying dates, peaking in the early dry season (June).

Dromadidae Crab Plovers

Dromas ardeola Crab Plover M-P&G 335 Category (2).

Mackworth-Praed & Grant (1957) state, on the basis of a flying juvenile seen by Pitman (card), that the Crab Plover is reported to breed near Kilifi and Sabaki in July to September. Until there is evidence that this species breeds within our limits this statement should be disregarded. Flying young are often seen at Mida Creek in August, and are there fed by adults.

Burhinidae Thicknees or Stone Curlews

Burhinus senegalensis Scnegal Thicknee M-P&G 261 Category (5) 7 records.

Burhinus capensis Spotted Thicknee M-P&G 262 Category (7) 38 records.

In Region D breeding is quite widespread but tends to peak in the short rains October-November, and again in the long rains March-May. In Region C the clear peak is in the late dry season September-October (10/15 records) and the few records for Region A are in the dry season.

Burhinus vermiculatus Water Thicknee M-P&G 263 Category (8) 81 records.

Numbers of records are adequate for analysis only in Region B, mainly on Lake Victoria, where there is a very clear and definite peak from August-October, especially September (51/65 records), in a drier break in the main rains though October is normally wet. In Region C all records except one are for the dry season. Region D records, some coastal, do not indicate a marked peak, but the main rainy season April-May is avoided. Region A records, although definitely stated, may be misidentification of B. senegalensis and indicate laying at the end of the dry season like that species.

Glareolidae Coursers and Pratincoles

Cursorius cursor Cream-coloured Courser M-P&G 325 Category (5) 7 records.

Region D. V, 1; VI, 4; VII, 1; VIII, 1 . 7

Breeds in the cool dry season after the long rains. MacInnes (1933-4) records a half-fledged young one near the Turkwell River, perhaps in Region A, but agreeing with other Region D records, on 22 September.

Cursorius temminckii Temmink's Courser M-P&G 326 Category (6) 20 records.

In Region C this courser breeds mainly June-July, in the dry season. Records from elsewhere are only indicative but include both wet and dry months, with no clear tendency.

Rhinoptilus africanus Two-banded Courser M-P&G 327 Category (7) 36 records.

The breeding season is widespread but in Region C peaks in the dry season June-August (10/16 records) and in Region D there is a peak from July-October, also dry (10/20 records). Dry seasons are preferred, especially the cool dry season in mid-year.

Rhinoptilus cinctus Heuglin's Courser M-P&G 328 Category (6) 17 records.

In Region C this courser breeds in the mid-year dry season like others and in Region D more records are for the mid-year dry season (4/7) but it also breeds in the wettest months, April and November.

Rhinoptilus chalcopterus Violet-tipped Courser M-P&G 329 Category (6) 11 records.

Indications are that this courser breeds in the cool dry season in Region C and prefers dry seasons elsewhere, or a break in the rains (Region B).

Glareola pratincola Common Pratincole M-P&G 330 Category (8) 73+ records.

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Region A. V, 2; VII, 2 . . . . 4
Region B. IV, 2; IX, 1 . . . . . 3
Region C. VI, 2; VII, 2; VIII, 3; IX, 3 . 10
Region D. IV, 19+; V, 28; VI, 3; VII, 6 56+
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In Region D breeds mainly in and just after the long rains: figures for colonies are often incomplete. In Region C breeds in the cool dry season June-September, but in Regions A and B may breed in the rains. Breeding in the rains may occur but may not be observed in Region D (Reynolds, pers.comm.)

Glareola nuchalis White-collared Pratincole M-P&G 333 Category (8) 81 records.

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Region A. I, 3; II, 1; III, 3; XI, 1 . . . 8
Region B. I, 4; II, 1; III, 5; IV, 2; V, 1; VI,
6; VII, 7; VIII, 23; IX, 17; X, 7 . . . 73
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All Region A records are in the dry season when rivers are lowest. In Region B breeding is widespread but peaks in August and September (40/73 records) which is late in a drier break between rainfall peaks.

Laridae Gulls and Terns

Larus hemprichii Sooty Gull M-P&G 348 Category (7) 35+ records.

Region E. VII, 15+; VIII, 15+; IX, 5+. 35+ All records show that this gull breeds at Kiunga chiefly July-August, at the height of the monsoon, with rough weather. However, its breeding cycle is also timed to coincide with that of several terns, on the eggs and young of which it feeds.

Larus cirrocephalus Grey-headed Gull M-P&G 342 Category (10) 919+ records.

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Region B. V, 112+; VI, 100+; VIII,

20+ . . . . . . 232+

Region D. III, 60; IV, 150; V, 283+; VI,

105+; VII, 20+; VIII, 64; IX, 5 . 687+
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Region B records are from Lake Victoria, all from one site where only approximate counts were made: numbers were certainly greater, and indicate breeding May-August, late in and just after the main rains, possibly peaking late May-June. In Region D breeding (mainly at Lakes Elmenteita, Naivasha and Nakuru) begins in March, increases in April, and peaks in May, late in the long rains, continuing into June, early in the cool dry season. The August and September records, in the dry season, are from Lake Manyara. Better data are needed from Massambwa Island, Lake Victoria, where thousands of pairs may breed. Pitman believed that movements of Haplochromid fish, coinciding with the rains, might influence breeding seasons, but it seems most likely that the onset of the main rains triggers breeding, and that if this is associated with food supply this has yet to be quantitatively proved.

Anous stolidus Common Noddy M-P&G 363 Category (9) 550-650 records.

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Region D (Latham Is.) XI, 300–400
Region E. V, 5+; VI, 7; VII, 20+; VIII,
210+; IX, 8 . . . . . . . 250+
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In Region E, on Tenewe Island near Lamu, breeding poaks in August, at the height of the monsoon rough weather. At Latham Island near Dar es Salaam eggs were found on 19 November 1971, when seas were comparatively calm. Only a small proportion of the noddies present had laid (Gerhart & Turner 1978). It appears that on islands near shore, breeding occurs only in rough weather, mainly July-August, but that at Latham Island other factors may be more important: inaccessibility is possibly the keynote.

Sterna caspia Caspian Tern M-P&G 350 Category (3).
Region D. III-IV

This tern is recorded breeding at Lake Turkana by Mackworth-Praed & Grant (1957) but there are no more recent records and the original cannot be traced; the period mentioned would coincide with the heaviest rain or end of the hottest dry season. Begging young have recently been seen in November, suggesting possible laying in September Hopson & Hopson (1975).

Sterna bergii Swift Tern M-P&G 355 Category (9) 500+ records.

Region D. (Latham Is.) X, 200–500; XI, 200–300 400–800

First definitely recorded breeding on Latham Island on 19 November 1971, when all nests contained eggs. Suspected breeding on other earlier occasions. In November 1972, 200–500 pairs had young about a week old, indicating laying in October. All available records indicate peak laying October-early November, when seas are calm (Gerhart & Turner 1978).

Sterna dougallii Roseate Tern M-P&G 352 Category (10) 20 500+ records.

Region D. VII, 50; VIII, 100 . . . 150(est.) Region E. VIII, 20 350+ . . 20 350

All records are for the Kiunga Islands, Whale Island off Mida Creek, and in one year at Shimoni. There is one record also for near Dar es Salaam (Thomas & Elliott 1973). A few pairs may lay in July, but peak laying undoubtedly occurs in mid—late August, when seas are rough at the height of the monsoon. Laying has also been found to coincide with neap tides at Whale Island, making it less accessible at low water. All available evidence indicates that rough seas are the most important factor dictating breeding dates. Breeding is very irregular, not occurring at all in some years, and with large fluctuations in numbers (8000 to 70) in successive years in the same site.

Sterna repressa White-cheeked Tern M-P&G 353 Category (10) 1704+ records.

Region E. VII, 43; VIII, 1221+; IX,

40+; X, 400 1704+

Records are in some cases (e.g. Fogden 1964) rather indefinite as to exact laying dates, but all recent records show that this tern, breeding in mixed colonies with *S. dougallii* lays mainly at the same time, in August, at the height of the rough monsoon seas, and presumably for the

same reasons. The October record, also from near Kiunga, is puzzling and does not accord with any other receni records. In this species also wide fluctuations are noted in numbers from year to year in the same site (100-725); numbers may be greater in years when S. dougallii does not breed abundantly.

Sterna anaethetus Bridled Tern M-P&G 359 Category (9) 300+ records.

Region E. VII, 49+; VIII, 250+ . 299+

Records suggest that on the Kiunga Islands and elsewhere in northern coastal Kenya this tern lays a little earlier than S. dougallii or S. repressa, beginning before the end of July but peaking like the others in August. Again, numbers evidently vary from year to year.

Sterna fuscata Sooty Tern M-P&G 358 Category (10) 65 000 + records.

Region D. (Latham Is.) X-XI,

60 000+ 60 000+

Region E. (Tenewe Is.) VII-VIII,

5000+ 5000+

This tern breeds in very large numbers (25000–60000 mentioned) at Latham Island, laying in October continuing into November (Gerhart & Turner 1978). At Tenewe Island laying begins in July, continuing into August. Thus, on northern Kenya offshore islands laying coincides with very rough seas, but at Latham Island occurs when the seas are calm. Again, this suggests that on islands near the coast rough weather dictates the laying date, while on distant inaccessible islands other factors may operate.

Childonias hybridus Whiskered Tern M-P&G 362 Category (7) 83 records.

Region C. V, 1; VII, 3; XII, 12 . . . 16 Region D. I, 30; V, 7; VI, 15; VII, 15 . . 67

This species probably breeds more commonly than supposed on weedy inland lakes not accessible without a boat. Dates are rather conflicting, the largest number in Region C being one record of 12 in December (1ains) with others in May and July (dry). In Region D most records are from Lake Naivasha, where laying occurs May–July, after the long rains and into the cool dry season, probably peaking in June, though exact counts were not made monthly. There is one record for Lake Eluanata near Arusha of 30 pairs in January, after the short rains, suggesting that in Region D breeding may occur late in or just after both rainy seasons.

Rhynchopidae Skimmers

Rhynchops flavirostris African Skimmer M-P&G 364 Category (8) 79+ records.

 The Region D records, all from Lake Turkana, indicate laying just before the main rains, peaking in April, the height of the rains, continuing into May; there may also be breeding in the subsequent cool dry season, July—August, but eggs have not been seen then. In southern Tanzania breeding begins in June, when sandbanks emerge from receding rivers, and probably peaks in July; there is one record for May from the Rovuma River, possibly in an early dry season. The single Uganda record, from Butiaba is for the rains. Thus on lakes with relatively stable shorelines the rains are preferred, but on river sandbanks Skimmers must breed in the dry season.

Pteroclidae Sandgrouse

Pterocles exustus Chestnut-bellied Sandgrouse M-P&G 369 Category (7) 24 records.

All records indicate breeding in the late rains and dry season, with a marked peak May-June in Region D, at the end of the long rains and early cool dry season.

Pterocles decoratus Black-faced Sandgrouse M-P&G 370 (7) 24+ records.

This species has a less concentrated breeding season than *P. exustus* but also breeds in dry months, with a peak June-August in Region D.

Pterocles gutturalis Yellow-throated Sandgrouse M-P&G 372 Category (7) 34+ records.

Breeds in dry months, with a concentrated peak June-August both in Region C and D. Some records are from close to the boundary of these regions, but the result is similar; also reputed to breed in January in Kenya (Mackworth-Praed & Grant 1957), also a dry month.

Pterocles lichtensteini Lichtenstein's Sandgrouse M-P&G 373 Category (4) 3+ records.

Scanty records indicate laying in a dry break in main rains or in dry months.

Pterocles quadricinctus Four-banded Sandgrouse M-P&G 375 Category (4) 3 records.

The only records are for the dry season. (All records for all species of sandgrouse indicate peak breeding in dry seasons.)

Columbidae Pigeons and Doves

Columba unicincta Afep Pigeon M-P&G 382 Category (3).

Said to breed Uganda March-April (Mackworth-Praed & Grant 1957).

Columba guinea Speckled Pigeon M-P&G 379 Category (7) 34 records.

Adequate records from Region D indicate breeding in almost all months, with no very marked peaks, but most (13/19) records in dry months. Some preference for dry months is also noticeable elsewhere. The bird is often associated with human habitations and food supply is unlikely to limit breeding in many areas. Reported to breed continuously at Mau Narok, rearing one brood after another, in buildings recently colonised (Sessions: cards).

Columba arquatrix Olive Pigeon M-P&G 380 Category (6) 18 records.

Region D records indicate preference for dry months (7/11) but most records from Region A are in wet months. Records not precisely dated from the Zaire-Uganda border (Region B) are for November-March, all dry. The species is a semi-nomadic fruit-eater.

Columba delegorguei Bronze-naped Pigeon M-P&G 383 Category (4) 1 record+.

The few available records (all pre-1934) suggest breeding both in dry and wet months.

Streptopelia lugens Dusky Turtle Dove M-P&G 385 Category (7) 25 records.

Data from near Nairobi suggest a marked peak May-June at the end of the long rains, but some breeding in many months. Elsewhere breeding occurs both in wet and dry months. The general statements in Mackworth-Praed & Grant (1957) that it breeds in Kenya and Uganda March-May and again November-December, i.e. in both rainy seasons, and in Tanzania February-April and again July-September are not borne out by recent dated records.

Streptopelia semitorquata Red-eyed Dove M-P&G 389 Category (9) 138+ records.

Data from Region D, mainly near Nairobi and from Arusha National Park, show breeding in all months, with least at the height of the long rains (April) and a fairly definite peak May-July after the long rains. Region B also shows breeding in most months with no very clear peaks. In Regions A and C inadequate records indicate widespread breeding both in wet and dry months. The data broadly confirm the published view that it breeds almost yearround, but, where adequate, suggest there may be more breeding late in or just after rains.

Streptopelia decipiens Mourning Dove M-P&G 387 Category (7) 26 records.

Data from Region B indicate widespread breeding but suggest a peak May-June, just after the wettest months. Elsewhere (Regions A, C, D) all but one record are for dry seasons.

Streptopelia vinacea Vinaceous Dove M-P&G 390 Category (4) 3 records.

The only records are Pitman's from Uganda, indicating breeding in a break in the main rains, but inadequate for any analysis.

Streptopelia capicola Ring-necked Dove M-P&G 388 Category (8) 61 records.

Data are not really adequate for any region but in Regions B, C, D all indicate very widespread breeding with no very obvious peaks except May-August in Region D (12/20 records). General notes by Jackson (1926) suggest a very marked peak in Region A in August-September,

but recent dated records do not support this.

Streptopelia senegalensis Laughing Dove M-P&G 392 Category (8) 81 records.

Although breeding is widespread, the peak laying months are clear in this small dove. In Region C most clutches are laid in the dry season May-October (22/33), and Whybrow (1948) records 20 nests between late March and July. In Region D there is a marked peak after the long rains, May and June (18/38 records) and, in Tsavo Park at least, another smaller peak in January, after the short rains. There are no dated records for Region A or E, but Jackson (1926) states that it breeds commonly in Region A in August-September, a break in the heaviest rains. Thus, this dove, on available evidence, breeds most just after the rains and into the dry season, but the same nest may be used for successive broods if one fails.

Oena capensis Namaqua Dove M-P&G 393 Category (6) 13 records.

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      Region A. III, 1; IX, 1
      .
      .
      2

      Region B. III, 1; IV, 1; V, 1
      .
      .
      3

      Region C. VIII, 1; IX, 1
      .
      .
      2

      Region D. V, 2; VI, 2; VII, 1; IX, 1
      .
      6
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The rather scanty records for any region, with two exceptions in Region B, indicate peak breeding late in the rains or in the dry season.

Turtur tympanistria Tambourinc Dove M-P&G 394 Category (8) 68 records.

Adequate records for Region B indicate widespread breeding but with strong peaks in March (end dry season) and August-September late in a break between rains. In Region D most records are in or just after the long rains, indicating a preference for wet months in relatively low rainfall areas. In Regions C and E most records are for dry months. This dove may well vary in its requirements in low or high rainfall areas.

Turtur afer Blue-spotted Wood Dove M-P&G 395 Category (8) 75 records.

The good data from Region B indicate breeding in every month with a peak July-August and another January-February, in dry seasons or in the break between the main rains. There are more records for dry or predominantly dry than for wet months. Records elsewhere are inadequate, but are for dry months.

Turtur chalcospilos Emerald-spotted Wood Dove M-P&G 397 Category (7) 36 records.

Data from Region D indicate a peak late in and after the long rains (9/17 records): in Region C inadequate records suggest a preference for wet months, and in Region E there may be a peak at the end of the main rains in May.

Aplopelia larvata Lemon Dove M-P&G 398-9 Category (6) 18 records.

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Region B. II, 1; IV, 2; V, 4; VII, 1 . 8
Region D. I, 1; III, 2; IV, 1; V, 2; VII, 2;
VIII, 1; IX, 1 . . . . . . . . . 10
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Scanty records indicate rather widespread breeding with no clear peaks in Region D; in Region B perhaps a peak in the main rains, in May.

Treron australis Green Pigeon M-P&G 401-403 Category (8) 62 records.

Records from all regions suggest widespread breeding but with a preference for dry months (15/19 Region B; 17/27 Region D), but there may be a peak November–February in Region D (19/27 records).

Treron waalia Bruce's Green Pigeon M-P&G 400 Category (4) 3 records.

Region A. IV, 2; V, 1 3
The few records are for the wettest months of the year.

Psittacidae Parrots

Poicephalus gulielmi Red-fronted Parrot M-P&G 444 Category (4) 2 records.

Only two dated records exist. Also said to breed in highland Kenya forests June and September-November; in Kenya (Region A) recently fledged young in May probably indicate laying in March.

Poicephalus cryptoxanthus Brown-headed Parrot M-P&G 445 Category (4) 4 records.

The very few dated records indicate breeding at the end of main rains.

Poicephalus meyeri Brown Parrot M-P&G 449 Category (4) 4 records.

The few dated records indicate dry season breeding: said to breed in Tanzania from July onwards; northern Uganda (Region A) September; and Kenya (Region A) December (Mackworth-Praed & Grant 1957).

Poicephalus rufiventris Orange-bellied Parrot M-P&G 448 Category (3).

No good dated record exists: reported to breed in Tanzania in March and to feed young in July and October (Mackworth-Praed & Grant 1957). One card suggests breeding in Kenya in June-July.

Psittacus erithacus Grey Parrot M-P&G 442 Category (4) 5 records.

Region B. I, 1; II, 2; VI, 1; VII, 1 . . . 5

The records are all for the dry season, or a drier break after the main rains.

Psittacula krameri Rose-ringed Parrakeet M-P&G 450 Category (3).

No dated records: said to breed Zanzibar in July-October (Mackworth-Praed & Grant 1957).

Agapornis pullaria Red-headed Lovebird M-P&G 452 Category (4) 4 records.

Region B. IV, 2; VI, 1; X, 1 4
Stated by Jackson (1938) to breed at Entebbe May-July.
Dated records cover only part of this period, which is at the end of the main rains.

Agapornis fischeri Fischer's Lovebird M-P&G 454 Category (6) 12+ records

Region C. I, 1; IV, 2; VI, 1+; VII, 3+ . 7+ Region D. I, 1; II, 2; VII, 2 . . . 5

Dated records are almost all for dry months, or the very end of the rains in Region C.

Agapornis personata Yellow-collared Lovebird M-P&G 455 Category (6) 18+ records.

Region C. III, 1; IV, 4; VII, 5+ . . 10+ Region D. III, 1; IV, 1; VI, 4; VIII, 2+ 8+

In Regions C and D mainly in dry months: numbers given are minimal as this species breeds in groups, and only a few are actually recorded.

Musophagidae Turacos, Go-away Birds and Plantain-eaters

Tauraco schuetti Black-billed Turaco M-P&G 430 Category (4) 2 records

Tauraco livingstonei Livingstone's Turaco M-P&G 427-8 Category (3).

No accurately dated records exist. Stated by Mackworth-Praed & Grant (1957) to breed in Tanzania September-November and on the Mara River (Region C) in Kenya July and October; this applies to the race formerly known as T. schalowi marungensis, now merged with livingstonei.

Tauraco fischeri Fischer's Turaco M-P&G 431 Category (4) 1 record.

The only dated record is that of Britton & Britton (1976). Young birds just out of the nest are recorded from Tanzania (Mackworth-Praed & Grant 1957) suggesting laying also in February and September.

Tauraco hartlaubii Hartlaub's Turaco M-P&G 432 Category (7) 27 + records.

Region A. VI, 1+; VII, 1+; XI, 1; XII, 1 4+ Region D. I, 2; III, 2; IV, 1; V, 2; VI, 2; VII, 3; VIII, 3; IX, 5; XI, 3 . . . 23

The only turaco with sufficient records for analysis, these suggest very widespread breeding with no very clear peaks, though July-September, in the cooler dry season, may be favoured in Region D (11/23 records). Failures are very common, and evidently pairs which have failed may quickly repeat. Many records are from gardens near Nairobi where this species undoubedly feeds largely on introduced fruits of e.g. Cotoneaster. Availability year-round of such fruit may distort the pattern in the wild state.

Tauraco leucolophus White-crested Turaco M-P&G 433 Category (3).

No good dated records exist, but it is reported to breed in northern Uganda May-June (Mackworth-Praed & Grant 1957).

Tauraco porphyreolophus Violet-crested Turaco M-P&G 434 Category (4) 2 records.

The only dated records are for the height of the rains near Iringa. Mackworth-Praed & Grant (1957) state that it breeds in southern Tanzania January-February (rains) and in Kenya March-April (dry).

Tauraco johnstoni Rwenzori Turaco M-P&G 435 Category (4) 1 record.

Region B. V, 1

The only dated record is of a sketch of a young bird found in June 1948 by Dr Lundholm and sent to Dr

V. G. L. van Someren. Mackworth-Praed & Grant (1957) state that it breeds on Rwenzori in December.

Musophaga rossae Ross's Turaco M-P&G 436 Category (6) 13 records.

Where data are at all adequate they indicate widespread breeding; recent work (M. Candy, unpub.) suggests that, like *T. hartlaubii* this species breeds repeatedly following nest failures or rearing of a brood, but may have a preference for breeding October-February in the dry season.

Corythaixoides concolor Go-away Bird M-P&G 439 Category (4) 2 records.

Corythaixoides personata Bare-faced Go-away Bird M-P&G 441 Category (5) 8 records.

Region B. V, 2; IX, 1; XI, 1. 4
Region C. V, 1; VIII, 1; IX, 1; X, 1. 4

Scanty data suggest a preference for dry-season breeding in Region C, but in Region B records include wet months.

Corythaixoides leucogaster White-bellied Go-away Bird M-P&G 440 Category (5) 6 records.

The very scanty data for this abundant and obvious species suggest that it prefers dry months, but will also breed in wet weather. Mackworth-Praed & Grant (1957) give March-June in nothern Uganda (wet) and March-April in southern Kenya (early rains). More data should be relatively easy to obtain for this species.

Crinifer zonorus Eastern Grey Plantain-eater M-P&G 438 Category (6) 15 records.

Data from Region B indicate preference for dry months (8/12 records) but it also breeds in the rains. The only records for Region A are for the end of the rains and Mackworth-Praed & Grant (1957) say it breeds in Tanzania (Region C) in October, late in the dry season.

Corythaeola cristata Great Blue Turaco M-P&G 437 Category (6) 20 records.

Region B. I, 2; II, 2; III, 4; IV, 1; V, 1; VI, 2; VII, 2; IX, 3; XI, 2; XII, 1 . . . 20

Available records, all from one region, indicate widespread breeding with 11/20 records in dry months and another four in a break in the main rains. Recent data (M. Candy, unpub.) indicate repeated breeding following nest-failure or rearing a brood. Note. All available data for the Musophagidae tend to indicate rather widespread breeding, with repeats if a nest fails, but more detailed dated data may show a marked preference for breeding in drier months.

Cuculidae Cuckoos and Coucals

Clamator glandarius Great Spotted Cuckoo M-P&G 413 Category (7) 21 records.

Region A. II, 1; III, 1; IV, 1 .	•	3
Region B. III, 2; IV, 1		3
Region C. IV, 2; X, 1; XII, 5		8
Region D. VI, 2; XI, 3; XII, 2		7

Region A and B records are for the dry season or early rains, Region C for early or late rains, and Region D mainly for the short rains. Records for each egg have been counted as separate; thus 5 for December in Region C were in the same nest. This Cuckoo necessarily breeds at the same time as its main hosts, the Pied Crow Corvus albus or Spreo spp.

Clamator jacobinus Black & White Cuckoo M-P&G 415 Category (6) 11 records.

Records are mainly in rainy months, when the hosts (bulbuls and babblers) may be expected to breed. A few eggs may have been misidentified, and could be attributed to *G. levaillantii*.

Clamator levaillantii Levaillant's Cuckoo M-P&G 414 Category (5) 8 records.

Records are all from babblers' (*Turdoides*) nests in the rains except one oviduct egg in Region C. Mackworth-Praed & Grant (1957) state that it breeds in Tanzania (Region C or D) in March-April, which would be wet months in either region. Breeding dates would coincide with those of the babbler hosts, peaking in the rains (see later, under *Turdoides* spp.)

Cuculus solitarius Red-chested Cuckoo M-P&G 406 Category (7) 31 records.

Most records are for wet months, when the hosts (Cossypha spp., Motacilla spp. etc). are breeding. In both Regions B and D there is a marked peak in the main rains, April-May.

Cuculus clamosus Black Cuckoo M-P&G 407 Category
(3)

No good recent dated records exist. Oviduct eggs from

Region C (Tanzania) in March and April suggest laying in those months. One was seen robbing a *Pycnonotus barbatus* egg at Naivasha (Region D) in April 1970. Mackworth-Praed & Grant (1957) state that it is recorded breeding in Uganda April-October and in Tanzania May; accurate data are needed.

Pachycoccyx audeberti Thick-billed Cuckoo M-P&G 412 Category (3)

There are no dated records, but Friedmann (1948) reported a female with an oviduct egg at Muniuni, Tana River (Region E) on 9 November ready to lay.

Gercococcyx montanus Barred Long-tailed Cuckoo M-P&G 411 Category (3).

No recent dated records exist: Moreau & Moreau (1939) and Sclater & Moreau (1932–3) record oviduct eggs and one laid November; Mackworth-Praed & Grant (1957) in addition give breeding at Amani September. These dates cover the short rains.

Chrysococcyx klaas Klaas' Cuckoo. M-P&G 418 Category (7) 26 records.

Most records are for wet months, when most of the hosts (chiefly sunbirds) are breeding (15/26 records). However, some breeding occurs in dry seasons also. Unfortunately some authorities (van Someren 1956) who have found several nests do not give exact dates. A few records for this cuckoo in *Ploceus* spp. nests have been discarded because of possible confusion with *C. caprius*.

Chrysococcyx caprius Didric Cuckoo M-P&G 417 Category (7) 22 records.

Some records have been discarded because of doubt of identity, with an unlikely host. Region D records indicate a clear peak in the long rains March-June when most ploceids breed, with some breeding also in the short rains.

Chrysococcyx cupreus Emerald Cuckoo M-P&G 416 Category (6) 17 records.

Shows a clear peak in the long rains in Region D, when hosts breed, with some breeding also in the short rains. In Region B also said to breed March (Seth-Smith 1913) and later, to October (Mackworth-Praed & Grant 1957).

Ceuthmochares aereus	Yellowbill	M-P&G 424 Category
(4) 3 records.		
Dogion P VIII	V .	

The Region D record is coastal (Dar es Salaam); the species seems mainly or entirely a migrant to the Kenya coast.

Centropus toulou Black Coucal M-P&G 420 Category (4) 3 records.

The few dated records include both wet and dry months.

Centropus monachus Blue-headed Coucal M-P&G 421 Category (5) 10 records.

Records suggest widespread breeding in both wet and dry months.

Centropus senegalensis Senegal Coucal M-P&G 422 Category (4) 5 records.

Region A. III, 1; IV, 3; V, 1 5 Even these few records suggest a clear peak at the

height of the rains.

Centropus superciliosus White-browed Coucal M-P&G 423 Category (8) 65 records.

Where adequate, data indicate widespread breeding, but with peaks in wet seasons: May and September-October Region B (15/20 records) and April-May and November-December Region D (16/30 records). The data confirm the more general statements of Jackson (1938) and Mackworth-Praed & Grant (1957) to the effect that in Kenya and Uganda the species breeds in both rains, April-May, November-December. There may be a tendency to nest most at the end of the rains (April in Region C and October in Region B). However, more data are needed to establish this possible peak.

Note. In all species of parasitic cuckoos there may be difficulty in identifying eggs in nests, or young being reared by hosts. In this analysis such doubtful records have been discarded; but further experience may indicate they were correct and should be included in any future analysis.

Tytonidae Barn and Grass Owls

Tyto alba Barn Owl M-P&G 528 Category (7) 27 records.

Most records are for dry months, with a marked peak in Region D in June and a smaller peak in September. However, one Region B record and several for Region D are in wet months.

Tyto capensis Cape Grass Owl M-P&G 529 Category (4) 4 records.

The few records are all for dry months.

Strigidae Owls

Otus scops Scops Owl M-P&G 534 Category (3)

There are no good dated records either on cards or in the literature for this common species. One card from Arusha suggests laying in September (dry).

Otus rutilus Pemba Scops Owl M-P&G 535 Category (3)
Said to breed on Pemba Island August-October
(Mackworth Praed & Grant 1957). The present status of
this species is unknown.

Otus leucotis White-faced Scops Owl M-P&G 536 Category (4) 3? records.

No recent dated records exist except one probably misidentified card for young in Region D. If correctly identified, this and other dated records indicate breeding in dry months. However, Mackworth-Praed & Grant (1957) state that it breeds also in northern Uganda March-August (wet).

Bubo capensis Cape (Mackinder's) Eagle Owl M-P&G 541 Category (7) 32 records.

Region A. I, 3; II, 3; III, 1; VII, 1; VIII, 2; IX, 1; X, 8; XI, 4; XII, 6 29 Region D. II, 1; IV, 1; XII, 1 3

The good data given by Sessions (1972 and cards) show a clear peak in Region A (Mau Narok) October-February (24/29 records) in the dry season. Two of three records from Mt Kenya, Region D are also for dry seasons but one is for the height of the rains, and a few from Mau Narok indicate breeding also in the rains, though the months of April-June are avoided.

All records for Regions A, B and C are for the dry seasons. In Region D this owl breeds in both dry seasons, with a marked peak in September towards the end of the longer cool dry season. There are no records for predominantly wet months, but a secondary peak develops in December, the end of the short rains.

Bubo lacteus Verreaux's Eagle Owl M-P&G 544 Category (7) 29 records.

This species which usually breeds in old nests of other birds, not on the ground, lays both in wet and dry months. In Region D, some records (7/18) are in two wet months, 11/18 in six dry months, of which three are in June at the end of the long rains, suggesting an actual preference for laying in wet months. The species is more riverine than other *Bubo* spp. and eats *inter alia* frogs and hedgehogs *Atelerix* spp., the latter more active in wet periods (Brown 1965b).

Glaucidium perlatum Pearl-spotted Owlet M-P&G 538 Category (4) 2 records.

In addition to two recent dated records, Mackworth-Praed & Grant (1957) record young in Kenya in August, laying in July. The Region C record is for the wet season, that for Region D in the dry season.

Glaucidium capense Barred Owlet M-P&G 540 Category (4) 1 record.

No recent dated records on cards, but Mackworth-Praed & Grant (1957) record a female in breeding condition on Mafia Island (Region D) in September (dry), and Matzke & Matzke (1974) record three flying young fed by parents, in January 1974, suggesting eggs laid in November.

Ciccaba woodfordi African Wood Owl or Woodford's Owl M-P&G 533 Category (5) 7 records.

Most of the Region D records are from Zanzibar and

Pemba where Mackworth-Praed & Grant (1957) say it breeds August-November; these are probably the same records as we have analysed from Pakenham (1943) and Vaughan (1930). Most records indicate a preference for dry months, but some also in wet.

Asio capensis Marsh Owl M-P&G 532 Category (5) 7 records.

Region A. X, I I Region C. V, I I Region D. V, 2; VI, 3 5

The few records provide a clear indication that this owl lays at the end of the rains and rears young in the subsequent dry season, the mid-year cool dry season in Region D being preferred.

Caprimulgidae Nightjars

Caprimulgus pectoralis Fiery-necked Nightjar M-P&G 551 Category (5) 6 records.

Most Region B records are for the wet season; the single Region C record is at the end of the dry season.

Caprimulgus fraenatus Dusky Nightjar M-P&G 548 Category (6) 14 records.

There is a possibility that in some cases this species has been confused with *C. poliocephalus* or *C. pectoralis* but most Region D records are for Arusha National Park where both this species and *C. poliocephalus* occur. All records are for the dry season, or early in the rains (one each in April and November).

Comprimulgus donaldsoni Donaldson-Smith's Nightjar M-P&G 552 Category (4) 1 record.

The only definite record is for the end of the mid-year cool dry season. A large fledgling, killed by a car in Tsavo, with feathers still in sheath on 15 August 1976 suggests laying in July or possibly late June, (dry).

Caprimulgus poliocephalus Montane (Abyssinian) Nightjar M-P&G 558 Category (6) 16 records.

Records indicate a peak in the short rains in Region D, but almost as much breeding in September, in the height of the mid-year dry season; in other regions the few records are for dry seasons.

Caprimulgus natalensis White-tailed Nightjar M-P&G 557 Category (5) 10 records.

Widespread breeding, but avoiding the wettest months, and with a probable peak June-July in a break between heavy rains.

Caprimulgus inornatus Plain Nightjar M-P&G 556 Category (4) 1 record.

Region A. VIII, I I

There are no recent records, but a nestling was collected on Mt Elgon in September and Mackworth-Praed & Grant (1957) also state that it breeds in Region A (Eldama Ravine) in May, suggesting a preference for wet months.

Caprimulgus tristigma Freckled Nightjar M-P&G 554 Category (5) 6 records.

Region C records are for the end of the dry season and early rains and those from Region D for the late long rains and early dry season.

Caprimulgus fossii Gabon Nightjar M-P&G 560 Category (5) 10 records.

Region C. IX, 1; XI, 2; XII, 1 . . . 4
Region D. V, 1; VI, 1; IX, 1; XI, 3 . . . 6

Some records of this species may be attributable to *C. clarus*. Those from Region C indicate breeding early in the rains and for Region D in both rainy seasons, but sometimes in dry months.

Caprimulgus clarus Slender-tailed Nightjar M-P&G 565 Category (6) 20 records.

Owing to past confusion in nomenclature, which failed to recognise this as a good species, but attributed it, as a race, to either C. fossii or C. climacurus, some of the above records may apply to C. fossii (not C. climacurus). If accepted, they indicate a preference for breeding in the rains in Regions A, D and E, and in Region B breeding both in wet months and in the mid-year break between heavy rains.

Caprimulgus climacurus Long-tailed Nightjar M-P&G 565 Category (5) 8 records.

Region A records are for late in the dry season. In Region B for the wettest month and the mid-year rains break.

Note. In all Caprimulgus species other than C. climacurus identification is difficult and must be open to some doubt.

A few species inhabiting distinctive habitats e.g. C. tristigma (on rocks) are easier; but the best guide to identity is calls at night. We have tried to make allowances for possible mistakes in identification, but urge greater care on future observers.

Macrodipteryx longipennis Standard-winged Nightjar M-P&G 563 Category (7) 21 records.

Data indicate a very clear peak in the height of the dry season in Region A, probably similar in Region B.

Macrodipteryx vexillarius Pennant-winged Nightjar M-P&G 564 Category (4) 1 record.

There are no recent records, but Mackworth-Praed & Grant (1957) also state that it breeds in Tanzania September -December which agrees with our only dated record and data from further south.

Apodidae Swifts

Apus melba Alpine Swift M-P&G 640 Category (4) 1 record.

Brooke (1971) states that practically nothing is known about the breeding of this swift north of the Zambezi. Mackworth-Praed & Grant (1957) state that it breeds on Mt Kenya October, perhaps also August. The single dated record above is for one which was probably incubating at c.3500 m on the Aberdare Mountains, Kenya, in the short rains.

Apus aequatorialis Mottled Swift M-P&G 641 Category (3).

There are no dated records for eggs or young. However, Brooke (1971) records adults in breeding condition in Region A June-July (rains) and Region D in March, June and September (all dry months). Mackworth-Praed & Grant (1957) give February and March for Region D and June-July with young in November for Region C (Mbulu District). These records all suggest rather widespread breeding. However, observation at the Njorowa Gorge, near Naivasha (Region D) where it breeds in large numbers in inaccessible cracks, suggest peak breeding in both rainy seasons. Better data are badly needed, and should not be too hard to obtain, at least by inference (e.g. eggshells collected below cliffs would indicate hatching).

Apus niansae Nyanza Swift M-P&G 637 Category (7) 25+ records.

Region D. III, 15+; IV, 10+. . . . 25+

The only dated records (above) are for approximate numbers feeding young in Arusha National Park. Literature records (Brooke 1971; Mackworth-Praed & Grant 1957) suggest breeding in Region B in May, Region C December-January and Region D in March, May and June-September, all dates in or after rains. Observation of the enormous

numbers breeding at the Njorowa Gorge (Region D) again indicate breeding in both rains, probably with an extended season.

Apus barbatus Black Swift M-P&G 636 Category (4) 1 record.

The only dated record is for the rains. Specimens with enlarged gonads (Brooke 1971) suggest breeding May in Region A, December in Region C. and April, July and August in Region D; all are for rains or into the cool mid-year dry season, resembling A. miansae in this respect.

Apus horus Horus Swift M-P&G 645 Category (9) 123+ records.

This species breeds in colonies in banks, often using old holes of *Merops bullockoides*. Birds arrive in numbers just before breeding, at once occupy the holes, and lay in a short time. The few dated records of eggs are for the long rains, those for Region C being at Narok. Others are all for birds presumed feeding young. However, this is probably correct. It would be less difficult to obtain better data for this swift than for some others, as colony occupation is clearly defined.

Apus caffer White-rumped Swift M-P&G 644 Category (8)-(9) 58+ records.

Where data are adequate (Regions B and D) they indicate a six month breeding season centred on a peak in the long rains (27/33 records Region B, March-June; 13/17 Region D, March-May). These figures suggest breeding beginning with the earliest rain and continuing after the height of the rains. Records for Regions A and C include both dry and wet months, with no clear peak discernible. Records for this species are better than for many because it breeds in relatively accessible nests of *Hirundo* spp.

Although there are no recent records from Region D for the short rains October-December, recent data disagree with Moreau's (1942) Amani studies. At Amani, in a forested area of Region D, Moreau recorded 94 clutches of which none was laid before 14 September or after 31 March. He unfortunately does not quantitatively date them so that we cannot include them above, but records six in September and eight in October in three years 1936-38. At Amani, evidently these swifts begin breeding at the end of the cool dry season, continue through the short rains, and end at the height of the hot dry season, in February and March. A series of broods, usually three, were reared each season in the same nest. The pattern of breeding in most parts of Region D and Region B is

similar, beginning just before the main rains and continuing afterwards, except that the seasons are different, recent records indicating a preference for the long rains rather than the short rains.

Apus affinis Little Swift M-P&G 643 Category (9) 82+&346+ records.

(b) Colonies roughly estimated

Data for this very abundant swift are difficult to obtain accurately owing to the inaccessibility of most colonies in buildings, under bridges etc., and the virtual necessity of destroying nests in order to ascertain their contents. Data from actual eggs or young indicate widespread breeding, peaking in rainy seasons, in both rains where two seasons occur. In one nest at Zanzibar successive layings were in September, December 1941; May, October 1942; January, May 1943 suggesting that breeding is more or less continuous by one pair whenever conditions suit.

More generally, Thomas (1960) gives October-April for Tanzania, the main rains in Region C; Moreau (1942) gives April-July, the long rains and just after for Amani (Region D); and Jackson (1938) May-July for Region D. Other literature references also indicate widespread breeding, peaking in the rains.

Although more precise data are needed, general observations indicate that this swift is stimulated to breed by the onset of the rains in any region, and may then rear a succession of broods. In coastal areas (Regions D and E) it is likely that breeding is almost continuous, individual pairs breeding again soon after rearing a brood at almost any time of year, with absences (in some cases) for a few weeks at a time (Pakenham 1945; L.H.B. pers, obs.).

Schoutedenapus myoptilus Scarce Swift M-P&G 639 Category (3).

No definite data exist. Birds in breeding condition have been collected in Region A in May and July, suggesting breeding in the rains, and individuals were seen going under overhangs on Mt Ololokwi (Region D) in July, suggesting breeding (L.H.B. pers. obs.).

Cypsiurus parvus Palm Swift M-P&G 646 Category (6) 12+ records.

In Region E definite records indicate breeding mainly from August-October, after the main rains, but one record is for the dry season. The only Region D record is for the dry season, but those for Region B are in the height of the rains. The literature suggests much more widespread breeding: Moreau (1941), Amani (Region D) late September to at least February, mainly dry; Jackson (1938), Region E March-June, in the rains, and Acholi March-April, early rains; Mackworth-Praed & Grant (1957), Region B March, April, and September-October (both rains); Region D, coastal December-January (dry) and Region E March-June (wet). More precise data are needed but available records suggest breeding in both wet and dry seasons.

Rhapidura sabini Sabine's Spinetail M-P&G 649 Category (3)

No nests are known, but specimens with enlarged gonads have been taken at Kakamega (Region B) in June, suggesting breeding in the rains.

Telacanthura ussheri Mottled-throated Spinetail M-P&G 647 Category (3).

Moreau & Moreau (1937) saw copulation in December, region D. Mackworth-Praed & Grant (1957) give breeding in Kenya April–May and Tanzania December-February (rains in both), but on what grounds is not stated. A record cited by Brooke (1971) for this species actually applies to *N. boehmi*.

Neafrapus boehmi Böhm's Spinetail, M-P&G 648 Category (4) 2 records.

The two dated records are both for the dry seasons, or end of the rains. That for Region E is for three young in an underground chamber at Sokoke, by A. D. Forbes-Watson, in late January-early February (year unknown) and must be accepted with some reserve: it has been wrongly quoted by Brooke (1971).

Coliidae Mousebirds

Colius striatus Speckled Mousebird M-P&G 566 Category (9) 226 records.

In Regions B and D, where data are adequate for good quantitative analysis, some breeding occurs in all months, but there are peaks in or just after the main or the short rains. In Region D 57/137 records are April-June and

another 22 from October–December. In Region B 36/65 records are from April–June. In coastal Region E, however, records suggest that the wettest months are avoided, most breeding occurring July–August, a mainly cool and dry period. Region A records span the rainy season but the few for Region C suggest the dry season is preferred. However, more records are needed from these single-season regimes. More general data given by, e.g. Mackworth-Praed & Grant (1957) are superseded by these more detailed records.

Colius leucocephalus White-headed Mousebird M-P&G 567 Category (4) 2 records.

Also reported to breed in August in Taita-Taveta (Region D) by Jackson (1938) quoting van Someren (1922). The two dated records are from the van Someren egg register from Maungu and Tsavo.

Urocolius macrourus Blue-naped Mousebird M-P&G 568 Category (8) 51 records,

The data closely resemble the pattern of *C. striatus*. In Region B there is a main peak May-June with 9/24 records, but some breeding in most months. In Region D there are peaks in or just after both rains 6/16 April-June and 7/16 October-November, probably fortuitous in favour of the latter. Region E records suggest a peak in July; Region A are all in the rains, and Region C in the dry season. Thus although the habitats of these two colies are very different their breeding pattern appears similar.

Trogonidae Trogons

Apaloderma narina Narina's Trogon M-P&G 570 Category (6) 13 records.

The records apparently exceed those for the rest of Africa combined. All are from the Nairobi area where the species is partially migrant in rather marginal habitat. They indicate breeding mainly in and just after the long rains with 9/13 records April-June: some breeding also in the short rains, if these are good. The same hole is used repeatedly.

Apaloderma vittata Bar-tailed Trogon M-P&G 571 Category (3).

There are no dated records but Mackworth-Praed & Grant (1957) record breeding in eastern Region D (Kilimanjaro, Amani) November-February in and after the short rains.

Alcedinidae Kingfishers

Ceryle maxima Giant Kingfisher M-P&G 466 Category (5) 8 records.

Region B. V, 1; VII, 3; X, 2 6
Region D. VI, 1; VII, 1 2

The few records suggest a peak of breeding in the midyear dry season or break in the rains. Mackworth-Praed & Grant (1957) also give September for Kenya. Records are few because of the difficulty of ascertaining contents in a very deep tunnel.

Ceryle rudis Pied Kingfisher M-P&G 465 Category (8) 67+ records.

Records are adequate for analysis only in Region B, where there is a marked peak in laying May-June and another, possibly representing a second brood, in September. Birds assemble at colonies in March just before the main rains and peak breeding occurs late in these rains, or in the break following, not in the wettest months. In Region C records suggest most breeding in the dry season, and in Region D, in or just after the long rains, April-May. However, records are inadequate for these regions. Data from Dar es Salaam (D, coastal) suggest breeding March-April but are inadequate for full analysis. Douthwaite (1976) shows that in Uganda this species feeds mainly on Haplochromis and Engraulicypris spp. but unfortunately gives no breeding dates.

Alcedo semitorquata Half-collared Kingfisher M-P&G 468 Category (5) 9 records.

Region D. I, 1; II, 1; IV, 1; V, 2; X, 4 . 9
Records indicate quite widespread breeding, perhaps peaking early in the short rains. Moreau (1944) says it is double-brooded at Amani, laying from late September-February, in and after the short rains.

Alcedo quadribrachys Shining-blue Kingfisher M-P&G 469 Category (5) 10 records.

Records indicate a marked peak at the height of the main rains (May,) but some breeding also in dry months.

Alcedo cristata Malachite Kingfisher M-P&G 470 Category (7) 25+ 1ecords.

Data indicate breeding in many months but with peaks in the rains April-May and December in Region D and less defined peaks in Region B. Jackson (1938) says it breeds at Naivasha May-June, after the main rains, and at Entebbe February-March and again September-

November, mainly in dry months. Recent data from Lake Nakuru (where there were no fish until 1961) indicate repeated breeding by the same pair in the same hole, another brood being started as soon as one had fledged (Reyer, unpublished).

Ispidina picta Pygmy Kingfisher M-P&G 471 Category (7) 21 records.

Data from Region B indicate widespread breeding, perhaps with a peak at the end of the rains: 9/16 records arc for dry or predominantly dry months.

Ispidina lecontei Dwarf Kingfisher M-P&G 472
Category (4) 2 records.

Region B. V. 1; VIII, 1 2

Mackworth-Praed & Grant (1957) also give breeding Uganda probably February and March which suggests a widespread breeding for this insectivorous species.

Halcyon senegalensis Woodland Kingfisher M-P&G 473 Category (5) 6 records.

The few records indicate breeding in or just after the main rains.

Halcyon senegaloides Mangrove Kingfisher M-P&G 474 Category (4) 3 records.

The nest and eggs of this species remain rather doubtfully described. One of the October records (Bangs & Loveridge 1933) is of eggs taken from a burrow in a bank. This suggests misidentification. The Region D record, from Zanzibar (Pakenham 1943) is for a nest in a hole in a tree, which seems a more likely site for this species.

Halcyon malimbica Blue-breasted Kingfisher M-P&G 475 Category (4) I record.

Region B. IV, I I

The only record is for the rains, in a tree termite nest

at Entebbe.

Halcyon chelicuti Striped Kingfisher M-P&G 479 Category (7) 21 records.

Records are inadequate for any region, but suggest rather widespread breeding in Regions B and D with a preference for dry months in Region D. Additional data are needed before any clear seasonal breeding can be attributed to this species.

Halcyon albiventris Brown-hooded Kingfisher M-P&G 476 Category (5) 9 records.

The few available records suggest a clear preference for dry-season breeding. Van Someren (1956) says that it nests in Region E May-July and November-December but gives no exact dates or localities.

Halcyon leucocephala Chestnut-bellied or Grey-headed Kingfisher M-P&G 477 Category (6) 26 records.

Region D records suggest widespread breeding (8/12 months) with most in the last quarter of the year October–December (7/12 records). Region A and Region C records suggest a preference for the early part of the rainy season, but all are inadequate for a good analysis.

Meropidae Bee-eaters

Merops superciliosus Madagascar Bee-eater M-P&G 482 Category (8) 71-81+ records.

There is only one certain record up to 1976, for Lamu Island (Serle 1943) supported by a skin. In Region D it is reported to breed on Mafia, Zanzibar and Pemba August-September. The Region B record, for the Kano Plains near Kisumu, was in a river bank and may have been misidentified as this species does not normally occur there except as a migrant, however, in view of later records we have accepted it. All other reported breeding localities are coastal, and in dry months. Bullock & Bullock (1976) have since published a record of a colony of 50 pairs in the bank of the Tana River near Adamson's Falls, Meru National Park, laying in August.

Merops nubicus Carmine Bee-eater M-P&G 484 Category (10) 2000+ records.

Region D IV (few); V (thousands).

There were no dated records in East Africa until 1976, when a large colony in flat ground on Ileret airstrip was recorded (Spoerry 1976). Data suggest thousands of pairs, laying early in May or perhaps late April. Spoerry also quotes von Hohnel who found large numbers breeding in flat ground in the same area in April 1894. The publication of these records stimulated the memory of others in 1976 when A.D. Forbes-Watson and R. E. Leakey recorded the end of the breeding season in July at Ileret. A.D. Forbes-Watson also quotes a nebulous record

by M. Cooper of tens of thousands breeding near Lokichoggio, Turkana, but gives no date. More recently, Hopson & Hopson (1977) have recorded a further colony of about 300 pairs at Andache, about half way between Ferguson's Gulf and Eliye springs, in stabilised sand dunes. Birds assembled at the colony at end of April, immediately after heavy rain; laid in May (all, apparently) and had reared young by early July. Eggs have not yet been collected in Kenya. However, the records show clearly that there are several breeding areas around Lake Turkana; that they are occupied in the main rains; that laying is mainly in May, and that in Kenya this bee-eater breeds normally in flat ground, not in vertical banks. The laying dates agree with those for Ethiopia just to the north (Urban & Brown 1971) where, however, colonies are found in vertical banks.

Merops albicollis White-throated Bee-eater M-P&G 488 Category (4) 5+ records.

The few definite recent records, mainly from near Magadi, indicate laying late in the dry season, feeding young early in the rains. The only Uganda record is for the height of the rains. Since these records were obtained, Hopson & Hopson (1977) have stated that in Turkana District west of Lake Turkana breeding of this bee-eater begins shortly after the first heavy rain, in April (no details given). The birds arrive in February, but no breeding occurs until after rains have fallen; young leave the nests in early April. In this area the species is a migrant, arriving in February, breeding, and leaving in September. Nests are single, in flat ground.

Merops pusillus Little Bee-eater M-P&G 488 Category (8) 64+ records.

Region A. II, 3; III, 2; IV, 2; X, I . . . 8
Region B. II, I; III, 3; V, I; VIII, I; VIII,
I; IX, 2; X, I; IO
Region C. II, I; VIII, I; X, 2; XI, 4; XII, I 9
Region D. IV, I; VII, I; VIII, I; IX, 2I+;
X, II; XII, I 36+
Region E. II, I I

Data from Region D suggest a marked peak at the end of the cool dry season and early in the short rains, with some breeding at other times. Region B records indicate widespread breeding, but mainly in dry seasons, Region A and C, mainly late in the dry season and into the early rains. Data in the literature (Mackworth-Praed & Grant 1957) do not substantially alter these conclusions. Probably this species breeds in many months, perhaps with peaks late in the dry season and into the rains, when abundant inseet food would be available for the young.

Merops variegatus Blue-breasted Bee-eater M-P&G 490 Category (4) 2 records.

 Merops oreobates Cinnamon-chested Bee-cater M-P&G 489 Category (8) 58+ records.

Data from Region D indicate a very clear peak October-January (38/45 records) in the short rains and just after, peaking in December. In Region A it also breeds from December-February, in the dry season and the few records for Region B are similar.

Merops revoilii Somali Bee-eater M-P&G 491 Category (4) 1 record.

Region D. V, I I

The only record is for a nest with young near El Wak,
June 1975.

Merops bulocki Red-throated Bee-eater M-P&G 492 Category (6) 10+ records.

Estimates are minimal. All dated records are for northern Uganda, where it breeds December-February, in the height of the dry season.

Merops bullockoides White-fronted Bee-eater M-P&G 493 Category (10) 508+ records.

Region A. I, 3+; II, 2+; also XII . 5+ Region C. X, 2; XI, 3+ . . . 5+ Region D. I, 75+; II, 200+; III, 1+; IV, 40+; VI, 30+; VII, 20+; VIII, 1+; IX, 1+; X, 72; XI, 16; XII, 42+; 498+

The records are unsatisfactory in that many observers have not recorded the numbers of occupied nests. However, they suggest a breeding peak in Region D October-February, in the short rains and into the following dry season, with considerable breeding also April-June in the long rains and into the cool dry season. Scanty records for Regions A and C are for dry months. Better quantitative data are needed, but it seems clear that this species prefers to breed in dry seasons.

Merops gularis Black Bee-eater M-P&G 495 Category (3).

No dated records exist: however, a pair were digging a hole in the Maramagambo Forest, Ankole, Uganda in March 1972, possibly about to breed in April (rains).

Merops muelleri Blue-headed Bee-eater M-P&G 494 Category (4) 3? records.

Region B. III, 1; IV, 1?; V, 1?; . . . 3?

The few dated records suggest breeding at the end of the dry season, or in the main rains.

Merops hirundineus Swallow-tailed Bee-eater M-P&G 496 Category (4) 1 record.

The only dated record is for early in the rains, Region A. In the same region birds have been seen excavating in March, indicating that laying may occur at the end of the dry season.

Coraciidae Rollers

Coracias abyssinica Abyssinian Roller M-P&G 458 Category (3).

Although no definite records exist, up to ten pairs were observed by J. Hopson (card) entering holes in termite mounds near Kalokol, Turkana (Region D) in April and May, following the rains, suggesting that this species breeds in the rains in northern Kenya, as in the southern Sudan and Ethiopia (Mackworth-Praed & Grant 1957, Urban & Brown 1971).

Coracias caudata Lilac-breasted Roller M-P&G 460 Category (6) 16 records.

Many records are inconclusive as to laying date, but indications are that this roller breeds both in dry and wet months with, in Region E, a strong preference for the dry or drier months after the main rains.

Coracias naevia Rufous-crowned Roller M-P&G 461 Category (4) 4 records

The few records suggest breeding in the rains; most nests are in banks.

Eurystomus glaucurus Broad-billed Roller M-P&G 463 Category (7) 22 records.

Most records indicate a strong preference for breeding in the rains, the main rains March-April in Regions A and B, and into the short rains September-November in Region D. Observations on this species indicate that breeding activity is initiated by the first good rains.

Eurystomus gularis Blue-throated Roller M-P&G 464 Category (3).

There are no records of definite egg dates, but it has been found 'breeding' at Mubende on 5 April and feeding a fledged young one in Budongo Forest 12 April 1972. These records indicate that in Region B it breeds early in the rains, like *E. glaucurus*; however, identification is difficult.

Upupidae Hoopoes Upupa epops Hoopoe M-P&G 518 Category (7) 22 records. Region B. I, 2; XII, 2 4	Bucerotidae Hornbills Tockus nasutus Grey Hornbill M-P&G 504 Category (6) 11 records. Region A. I, 1; II, 2
Region C. VIII, 2; IX, 2; XI, 1 5 Region D. III, 1; IV, 2; VII, 2; VIII, 1; IX, 2; X, 3; XI, 1; XII, 1 13 All records for Regions B and C are for the dry season. In Region D 7/13 records are for predominantly dry or dry months, but it also breeds in the rains, especially	Region D. I, 1; II, 2; III, 2; XI, 1; XII, 2 . 8 All Region A and D records are for the dry season or late in the short rains. Betts (1966) quotes a male feeding young or a female in Region C in January (rains). Evidently the dry season is preferred.
perhaps the short rains October-November. Better data are needed for this common and obvious species.	Tockus erythrorynchus Red-billed Hornbill M-P&G 505 Category (7) 22 records. Region A. V, 1; VII, 1; VIII, 1 3
Phoeniculidae Wood Hoopoes Phoeniculus purpureus Green Wood Hoopoe M-P&G 519 Category (6) 20 records. Region B. XI, I I Region C. I, I; III, I; IX, I; XI, I 4 Region D. I, I; II, I; IV, I; V, 3; VI, 2;	Region D. I, 1; II, 1; III, 3; IV, 2; V, 2; VI, 1; X, 2; XI, 4; XII, 3 19 Records indicate quite widespread breeding, but with a peak in Region D in the short rains October-December (9/19 records) and a smaller peak (7/19 records) in the long rains March-May.
VII, 1; VIII, 2; IX, 3	Tockus deckeni Von der Decken's Hornbill M-P&G 507 Category (6) 14 records. Region D. I, 1; II, 2; III, 2; XI, 5; XII, 4. 14 This species shows a very clear peak in the short rains, continuing into the following dry season: data for January-March, however, are from Moreau (1936) while all more recent dated records are for November-December.
Phoeniculus granti Violet Wood Hoopoe M-P&G 520 Category (4) 2 records. Region D. I, I; VII, I 2 If indeed this is a good species the few records from eastern Kenya are for dry months. Some may have been attributed to P. purpureus.	Tockus jacksoni Jackson's Hornbill M-P&G 507 Category (4) 3 records. Region A. IV, I; V, I
Phoeniculus bollei White-headed Wood Hoopoe M-P&G 522 Category (5) 9 records. Region A. II, 1; VI, 2; IX, 1; XII, 2 . 6 Region B. V, 1	Tockus flavirostris Yellow-billed Hornbill M-P&G 506 Category (4) 4 records. Region A. II, 1; III, 1
Phoeniculus minor Abyssinian Scimitarbill M-P&G 527 Category (5) 6? records. Region A. IV, I	Tockus fasciatus Pied Hornbill M-P&G 510 Category (4) 2? records. Region B. III, 1; V, 1?
Phoeniculus cyanomelas Scimitarbill M-P&G 522 Category (4) 5? records. Region C. VIII, 1; X, 1	Tockus alboterminatus Crowned Hornbill M-P&G 509 Category (5) 13 records. Region A. II, 1; IV, 1; VII, 1

D and E dry months are definitely preferred, chiefly September-October (6/8 records for these regions).

Geratogymna atrata Black-wattled Hornbill M-P&G 503 Category (3).

The only record is that of Keith (1970) recording a Crowned Eagle raiding a nest with young in January. Eggs might have been laid 4–5 months earlier-August of September.

Bycanistes subcylindricus Black & White Casqued Hornbill M-P&G 500 Category (6) 15 records.

Most of the records are from Kilham (1956) and recent cards. Although precise egg laying dates are hard to estimate in a species where the female is enclosed for four months, data from Region B indicate a clear preference for breeding in the dry season October-February, with only one record in August (a break in the rains).

Bycanistes brevis Silvery-cheeked Hornbill M-P&G 501 Category (4) 3 records.

There are no recent dated records for this hornbill, all the above being from Moreau (1936). Beesley (1973) surprisingly gives none. Moreau (1936) remarks that the breeding season appears distinct although fruit is available year-round (at Amani). Additional records are needed, but the few available indicate laying in the short rains and feeding young into the following dry season.

Bucorvus abyssinicus Abyssinian Ground Hornbill M-P&G 516 Category (6) 17 records.

Peak laying occurs at the height of the dry season January-March. (13/16 records) with very little breeding at any other time. This implies feeding young early in or into the main rains.

Bucorvus leadbeateri Ground Hornbill M-P&G 515 Category (5) 8 records.

There are fewer good dated records for this than for the last species. In addition, Mackworth-Praed & Grant (1957) record 'breeding' in Kanya March-June and Tanganyika July-August (eggs calculated from nestlings). The latter agree with our only recent record from Region C, in the dry season. Available records from Region A indicate laying in the dry season, and in Region D mainly in and after the short rains October-February.

Note. For all hornbills there must be doubt as to precise laying dates as the female enters the hole well before egglaying, and even in those species where data have been recorded there can be considerable variation.

Capitonidae Barbets and Tinkerbirds

Lybius bidentatus Double-toothed Barbet M-P&G 573 Category (6) 13 records.

Most records are for the dry season October-February in Regions A and B.

Lybius melanopterus Brown-breasted Barbet M-P&G 580 Category (6) 15 records.

Most records are for the short rains October-December or the dry season following, but some also for the long rains.

Lybius leucocephalus White-headed Barbet M-P&G 576 Category (6) 11 records.

The few records for this common and obvious species indicate breeding both in dry and wet months, perhaps with a mid-year peak May-June in Regions B and D.

Lybius guifsobalito Black-billed Barbet M-P&G 574 Category (4) 1 record.

The only dated record is for the end of the dry season. Also stated to breed in Uganda, January (Mackworth-Praed & Grant 1957) also dry.

Lybius torquatus Black-collared Barbet M-P&G 575 Category (4) 2 records.

Both dated records are for the dry season. Also stated to breed in Tanzania (localities not stated) by Mackworth-Praed & Grant (1957) October-December (late dry season?) and in eastern Tanzania (possibly Region D) January; dry season.

Lybius hirsutus Hairy-breasted Barbet M-P&G 582 Category (4) 2 records.

The few records suggest breeding in and after the main rains. Mackworth-Praed & Grant (1957) state that it breeds May-July in Region B.

Lybius melanocephalus Black-throated Barbet M-P&G 583 Category (4) I record.

The eggs of this common and widespread species are apparently undescribed. Said also to breed March-April, end dry season or early rains, in Region D by Mackworth-Praed & Grant (1957).

Lybius lacrymosus Spotted-flanked Barbet M-P&G 585 Category (8) 59 records.

The best documented of all tree-nesting barbets, this species has a widespread breeding season in Region D (10/12 months) but there is a peak in the hot dry season January-March (27/50 records) and another in September-October (10/50 records). The wettest months are avoided in Region D, but in Region C the few records suggest a preference for the rains. Region A and B records are for dry months. Jackson (1938) says it breeds October-November and February-March confirming this, and for Region C Mackworth-Praed & Grant (1957) record breeding in September-October (end dry season).

Lybius diadematus Red-fronted Barbet M-P&G 585 Category (7) 27 records.

Records for Region D indicate that dry months are preferred especially January–March, the hot dry season (9/14 records). Van Someren (1956) says that most breeding in this region occurs February–July occasionally later. Records for Regions C and B also suggest preference for dry months but most of the few records for Region A are in the rains, April–May.

Gymnobucco bonapartei Grey-throated Barbet M-P&G 586 Category (4) 5 records.

The few records indicate dry season breeding in Region A, but also in rains in Region B. Also said by Mackworth-Praed & Grant (1957) to breed in Region B March-April onwards (early rains).

Buccanodon leucotis White-eared Barbet M-P&G 588 Category (7) 24 records.

Almost all records are from the Arusha area, showing a clear peak in the short rains and into the subsequent dry season October–January (16/24 records) with some breeding also late in the cool dry season.

Buccanodon olivaceum Green Barbet M-P&G 589 Category (5) 7 records.

Region E. III, 1; VI, 1; IX, 2; X, 2; XI, 1. . 7

The above are all recent dated records suggesting a preference for the period September-March (dry). Also reported by van Someren (1932) to breed in May, June, July and December, dates which conflict with the recent data suggesting breeding mainly after the main rains in Region E. Mackworth-Praed & Grant (1957) record a young bird being fed at Amani (Region D) in December, laying probably November.

Buccanodon duchaillui Yellow-spotted Barbet M-P&G 590 Category (4) 5 records.

Region B. I, 1; II, 1; IX, 1; X, 2 . . . 5
Records indicate a preference for breeding in the main dry season October-February.

Pogoniulus scolopaceus Speckled Tinkerbird M-P&G 599 Category (4) 1 record

Pogoniulus leucomystax Moustached Green Tinkerbird M-P&G 592 Category (4) 3 records.

Scanty data suggest breeding in the long rains in Region D. In Region A (Mau Narok) the period of maximum calling is November-January, which would agree with the single dated record of eggs (Jackson 1938) in January, in the dry season.

Pogoniulus pusillus Red-fronted Tinkerbird M-P&G 594 Category (4) 3 records.

Although this is a very widespread and common species dated records are few. Mackworth-Praed & Grant (1957) also give February-May for southern Kenya (Possibly Region D). The few dated records are for dry seasons.

Pogoniulus chrysoconus Yellow-fronted Tinkerbird M-P&G 595 Category (3).

There is only one indicative record from Region B, suggesting laying in August, a bird possibly feeding young at Maseno in September.

Pogoniulus bilineatus Golden-rumped Tinkerbird M-P&G 597 Category (7) 21 records.

Region B. I, 2; II, 2; III, 1; VIII, 2 7
Region D. V, 3; VI, 2; XII, 1 . . . 6
Region E. IV, 1; V, 3; VI, 1; VII, 1; IX,
1; XII, 1 8

The only tinker-bird fairly well documented by dated records. In Region B most records are for the dry season, or a break in the rains, but in Region D in and just after the rains. In Region E breeding is widespread, but mostly after the main rains. Recent good observations in Region E (Britton: cards) confirm earlier indications that a series of broods are reared in the same hole. Jackson (1938) states that it breeds at Entebbe February-May and again August-December and, in Zanzibar (coastal Region D) in October-January (dry) and also April-May (wet). Mackworth-Praed & Grant (1957) say it breeds in the Kenya Highlands (Regions D or A) in March-May (wet) and east of the Rift (Region D) October-January, also April-May, in both dry and wet seasons. These more general statements tend to confirm a preference for dry months, but it also breeds in the rains.

Pogoniulus subsulphureus Yellow-throated Tinkerbird M-P&G 598 Category (4) 1 record.

There is only one definite dated record in the literature, though Mackworth-Praed & Grant (1957) say it breeds in Uganda May-June and again December-January, just after the main rains.

Trachylaemus purpuratus Yellow-billed Barbet M-P&G 604 Category (4) 5 records.

The available records indicate a preference for dry-season breeding but some also in the rains.

Trachyphonus vaillantii Levaillant's Barbet M-P&G 600 Category (4) 1 record.

The single dated record is from the Lake Manyara area (Beesley: card). Mackworth-Praed & Grant (1957), however, state that it breeds in southern Tanzania September-October, in the late dry season.

Trachyphonus darnaudii D'Arnaud's Barbet M-P&G 603 Category (5) 9 records.

 Region A. V, 1; IX, 1
 .
 .
 2

 Region C. IV, 1; VIII, 1; XI, 2
 .
 .
 4

 Region D. IV, 1; VI, 1; X, 1
 .
 .
 3

The above are definite dated records, usually from adults feeding young. Other more general references in the literature suggest breeding Region A April–May; Region C January–February, again April–June and also at other times (Jackson 1938, Mackworth-Praed & Grant 1957, Betts 1966). The dated records indicate a preference for wet months but some breeding also in dry weather. The difficulty is to ascertain the contents of the vertical nest hole and better records are needed.

Trachyphonus erythrocephalus Red & Yellow Barbet M-P&G 601 Category (6) 15 secords.

Records for regions A and C suggest a preference for the rains, but in Region D 6/12 records are for dry months, and 6/12 in the rains.

Indicatoridae Honeyguides

Note. The great difficulty of identifying adults of some of the smaller species must make records of young not actually collected open to doubt. Most definite records have been collated by Friedmann (1955). The species easiest to recognise with certainty are *Indicator indicator* and *Prodotiscus insignis*.

Indicator variegatus Scaly-throated Honeyguide M-P&G 606 Category (5) 7 records.

The records are all from Friedmann (1955) except a female collected with an oviduct egg (Britton and Sugg: card).

Indicator indicator Black-throated Honeyguide M-P&G 605 Category (6) 12? records.

The above include two eggs taken from nests of Myrme-cocichla aethiops probably of this species (Belcher: card). Unfortunately a good many records are vague, and dateless, notably those of van Someren (1916). In Region D there are dated records for 7/12 months, in both wet and dry periods. This best-documented honeyguide breeds for much of the year and has very varied hosts, so this is not surprising.

Indicator minor Lesser Honeyguide M-P&G 608 Category (5) 9-10 records.

The records, based mainly on van Someren (quoted by Friedmann 1955) are all rather indefinite, but indicate a preference for breeding in or just after the main rains, in barbet holes. This is somewhat strange as the barbet hosts tend to breed in the drier months rather than in the main rains. Better, more accurate dated records are needed.

Indicator meliphilus Pallid Honeyguide M-P&G 610 Category (4) 1 record.

There appears to be one definite record attributable to this species in Region B in June (nestling July, Friedmann 1955) recorded under the name I. exilis meliphilus.

Prodotiscus insignis Cassin's Honeybird M-P&G 613 Category (6) 12 records. Region A. IV, I	Dendropicos poecilolaemus Uganda Spotted Woodpecker M-P&G 626 Category (4) 4 records. Region B. I, I; VI, I; VIII, I; IX, I
Campethera nubica Nubian Woodpecker M-P&G 619 Category (6) 15 records. Region A. IV, 1	The best recorded of any woodpecker, Region B and D records indicate widespread breeding with no very obvious peaks and numbers of records about equal in wet and dry months. Region C records also include both wet and dry months.
Records are everywhere inadequate but in Region D are mainly in dry months (7/8 records) and the wettest months are avoided in Region B. However, the only good record for Region A is in the rains. Mackworth-Praed & Grant (1957) also record 'breeding' in Turkana (Region D or A) in May and in Region D, June.	Mesopicos griseocephalus Olive Woodpecker M-P&G 631 Category (4) 2 records. Region C. X, I I Region D. XII, I I The only definite dated records are for dry seasons, but Mackworth-Praed & Grant (1957) give August-November in Region D, including the short rains.
Campethera abingoni Golden-tailed Woodpecker M-P&G 622 Category (4) 3 records. Region D. I, 1; II, 1	Mesopicos xantholophus Yellow-crested Woodpecker M-P&G 632 Category (4) 2 records. Region B. VIII, 1; I, 1 2 One in rains, one in dry season.
Campethera tullbergi Fine-banded Woodpecker M-P&G 617 Category (4) I record. Region C. X, I I There is also a record from Mau Narok (Region A) of two young with adults in December suggesting breeding in November. The few records suggest dry season breeding. Dendropicos fuscescens Cardinal Woodpecker M-P&G	Thripias namaquus Bearded Woodpecker M-P&G 629 Catergory (5) 7 records. Region C. V, 1; VI, 1 2 Region D. I, 1; V, 3; VIII, 1 5 The records for Region C are in dry months, but Region D records suggest a peak late in the long rains. One record of fledged young in Region A suggests laying in October (dry), and Mackworth-Praed & Grant (1957) give June
623 Category (5) 9 records. Region B. I, I; V, I; VII, I	and August-November (dry) for Region C in Tanzania. Passeriformes
suggest a preference for dry season breeding in Region D, but also for the rains in Regions B and C. Mackworth-	Eurylaemidae Broadbills Smithornis capensis African Broadbill M-P&G 650 Category (4) 2 records

Category (4) 3 records.

Region C. XI, 2

Region D. XII, 1 .

Praed & Grant (1957) give 'breeding' in Region D, February

and October; C September-November, mainly in dry

months, but also probably April-May in Uganda (wet).

Smithornis rufolateralis Red-sided Broadbill M-P&G 651 Category (4) 1 record. Region B. VI, 1	Chersomanes albofasciata Spike-heeled Lark M-P&G-Category (4) 4 records. Region D. III, 1; IV, 2; XI, 1 4
Pittidae Pittas Pitta angolensis African Pitta M-P&G 652 Category (4) I record. Region C. XII, I I Two birds with enlarged ovaries in region E in July are unlikely to be breeding at this latitude or season (Britton & Rathbun 1978). Pitta reichenowi Green-breasted Pitta M-P&G 653 Category (4) 2 records.	Calandrella cinerea Red-capped Lark M-P&G 686 Category (7) 22 records. Region A. III, 1; IV, 2; V, 1; X, 1; XII, 1 6 Region B. VI, 2
~ · · · ·	Eremopterix leucotis for discussion.
Region B. V, 2	
The few broadbill and pitta records are all in the rains.	Calandrella somalica Rufous Short-toed Latk M-P&G
Alaudidae Larks	685 Category (6) 12 records.
Mirafra cantillans Singing Bush Lark M-P&G 654	Region D. III, 1; IV, 1; V, 7; VI, 3 . 12 Breeding in the long rains.
Category (5) 10 records.	
Region D. IV, 1; V, 5; VI, 4 10 Breeding in the long rains.	Calandrella personata Masked Lark M-P&G 689
	Category (4) 1 record.
Mirafra albicauda White-tailed Bush Lark M-P&G 655	Region D. V, I I
Category (4) 3 records.	
Region C. IV, 1; V, 1	Galerida fremantlii Short-tailed Lark M-P&G 678
Region D. III, 1 1	Category (5) 9 records.
	Region D. V. 2; VI, 7 9
Mirafra africana Rufous-naped Lark M-P&G 657, 659	Breeding late in the long rains.
Category (7) 39 records.	
Region B. II, 1; V, 2; VI, 2; XI, 1; XII, 2 8	Galerida cristata Crested Lark M-P&G 675 Category
Region C. I, 2; IV, 1; V, 1; VI, 1 5	(4) I record.
Region D. II, 1; III, 6; IV, 4; V, 7; VI, 2; VII, 1; XI, 3; XII, 2	Region D. III, I I
A rains breeder, especially in Region D. All Region C	
	Galerida malabarica Short-crested Lark M-P&G 676
records are from the north-west, at Narok and Serengeti.	Category (4) 1 record.
Minds of the second of the sec	Region D. V, I I
Mirafra rufocinnamoniea Flappet Lark M-P&G 660	
Category (6) 11 records.	Eremopterix leucopareia Fischer's Sparrow Lark
Region B. VI, 1; VII, 1; VIII, 1 3	M-P&G 682 Category (8) 51 records.
Region C. V, 1; XI, 1; XII, 2 4	Region B. V, 4; VI, 4 8
Region E. VII, 1; VIII, 1; XI, 1; XII, 1	Region C. IV, 2; V, 5; VI, 5; VII, 2; VIII, 2 16
These few records suggest that the breeding seasons are	Region D. II, 1; III, 1; IV, 3; V, 12; VI, 8;
ill-defined.	VII, 1; XII, 1
	Rains breeding in Regions B and D but dry season
Mirafra africanoides Fawn-coloured Lark M-P&G 661 Category (5) 6 records.	breeding in Region C (see discussion under next species).
Region C. I, I	E-material language Charten had a Community
Region D. IV, 1; V, 4 5	Eremopterix leucotis Chestnut-backed Sparrow Lark
These few records are confined to the rains.	M-P&G 679 Category (4) 2 records.
Minformation Philadelphia 11 11 PAG	Region D. III, 1; V, 1
Mirafra poecilosterna Pink-breasted Lark M-P&G 665	White (1959) and Benson (1963) have discussed the dry season breeding of this species, Calandrella cinerea and
Category (4) 3 records.	
Region D. III, 1; VI, 1; XII, 1 3	Mirafra nigricans, mainly in the southern tropics. Benson has shown that the dry season breeding of this species
Mirafra nigricans Dusky Bush Lark M-P&G 666, 667	is mainly confined to areas of higher rainfall which are
Category (4) 1 record	liable to flooding in the rains, whereas rains breeding is a
Region A. II, 1	feature of low rainfall areas which may be too dry and
	77

lacking in food at other times. Region D records of E. leucopareia and C. cinerea are in the rains. Most of these records are from Kenya, where E. leucopareia is a characteristic species of short-grass plains in semi-arid areas, and C. cinerea is typically a bird of short-grass plains and fallow fields at higher elevations, though both breed on the Athi plains at 1600 m. Flooding is a feature of the Chalbi Desert and other desert areas of northern Kenya but it is exceptional elsewhere, and most or all lark breeding is in the rains. Floods in desert areas are of short duration and breeding is likely to take place in the brief verdant period which follows. Similar dry season breeding in Region C contrasting with rains breeding in Region D is found in the Cinnamon-breasted Bunting Emberiza tahapisi and the Capped Wheatear *Oenanthe pileata*, both of which regularly or often occupy short-grass plains, though E. tahapisi is also a species of rocky or stony areas.

Hirundinidae Swallows, Martins, Roughwings Riparia cincta Banded Martin M-P&G 1070 Category (7) 22 records.

Riparia paludicola African Sand Martin M-P&G 1069 Category (7) 23 records.

In the southern tropics, where nesting sites in banks along perennial rivers are liable to flooding, breeding is in the dry season (Benson 1963). Both Region C records are in the dry season, but breeding elsewhere is in the rains, despite the fact that 11/14 sites are in river banks.

Hirundo angolensis Angola Swallow M-P&G 1055 Category (8) 56 records.

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Region A. III, 1; IV, 2; V, 2; VI, 13 . 18
Region B. I, 1; II, 2; III, 6; IV, 14; V, 2;
VI, 2; X, 1; XI, 1 . . . . . 29
Region C. I, 2; VIII, 1; X, 1; XI, 1; XII, 1 6
Region D. IV, 1; V, 2 . . . . . 3
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Breeding is virtually confined to the rains when insect life is abundant and mud for nest-building is readily available.

Hirundo atrocaerulea Blue Swallow M-P&G 1060 Category (4) 5 records.

Region C. II, 1; XI, 1; XII, 3. . . . 5 Breeding in the rains.

Hirundo smithii Wire-tailed Swallow M-P&G 1061 Category (9) 104 records.

Breeds in the rains in Region E but during most months in Regions C and D, though 47/61 Region D records are in and around the long rains February-July, peaking in May. Benson (1963) has suggested that the close association of this species with human dwellings probably accounts for its ill-defined breeding seasons, as mud is likely to be available around habitations at all seasons. However, this is not borne out by observations on the species' behaviour, which suggest that building is stimulated by the onset of rain, making mud readily available.

Hirundo aethiopica Ethiopian Swallow M-P&G 1057 Category (6) 19 records.

Region E. III, 2; IV, 4; V, 8; VI, 4; XII, 1 . 19

All nests were under coral overhangs or inside caves on the seashore, mainly in the rains. There are records of occupied nests on houses in Region D during the long rains April-May as well as a May record of a nest attached to an overhanging rock at a water-hole.

Hirundo semirufa Rusous-chested Swallow M-P&G 1064 Category (4) 3 records.

Hirundo senegalensis Mosque Swallow M-P&G 1063 Category (7) 37 records.

Hirundo daurica Red-rumped Swallow M-P&G 1062

Well-defined breeding seasons in the rains, peaking April-May in the long rains in Region D. This species is frequently associated with buildings, but is apparently stimulated to breed by the onset of rains.

Hirundo abyssinica Striped Swallow M-P&G 1 065 Category (8) 97 records.

Breeding is virtually confined to the rains, with a peak at the beginning of the long rains in Region B and a preference (26/41 records) for the long rains (March-June) in Region D. There are no Region B records after June, but there is a definite short rains peak in region D November-December. Like H. smithii and H. fuligula (see below) this species and H. daurica are closely associated with human dwellings, but they hardly breed outside the rains. They are larger species than either smithii or fuligula and probably take larger insects, the abundance of which may be more closely linked with wet periods.

Hirundo griseopyga Grey-rumped Swallow M-P&G 1066 Gategory (6) 12 records.

Dry season breeding in all regions, as also is the case in the southern tropics (Bensen 1963). The nest is a cup of grass in disused rodent burrews on dry plains, especially where the grass has been recently burnt off. Such nest sites are likely to be water-logged or flooded during the rains.

Hirundo fuligula African Rock Martin M-P&G 1073 Category (9) 112 records.

Region A. I, 2; II, 1; IV, 1; VI, 1; XII, 2 . 7
Region C. I, 1; II, 5; III, 4; IV, 1; VI, 1;
VII, 1; VIII, 1; IX, 3; X, 1; XI, 2; XII, 1 21
Region D. I, 2; II, 4; III, 8; IV, 15; V, 19;
VI, 6; VII, 3; VIII, 1; IX, 7; X, 4; XI, 13;
XII, 2 84

Breeding in all months in Region D and in all except May in Region C, but peaking March-June, September and November in Region D and February-March in Region C. Its close association with human dwellings (46/54 cards) may account for some at least of the dry season records (see discussion under *H. smithii*); however, on L.H.B's. house at Karen it breeds regularly in the rains or just after.

Psalidoprocne pristoptera Black Roughwing M-P&G 1075 Category (7) 46 records.

 Region D breeding is in all months except April, peaking in the short rains with 15/39 records November-December, when rains are likely to be less subject to violent floods than in April-May.

Psalidoprocne albiceps White-headed Roughwing M-P&G 1080 Category (6) 15 records.

Breeding is more or less confined to the rains. Typically this and the previous species nest in roadside banks or similar dry sites rather than in banks along rivers.

It appears that, where hirundines have a choice of long or short rains, they breed most often in the heavier rains. They breed in the rains in Region C irrespective of the presence of hordes of Palaearctic hirundines which share available food supplies and usually far outnumber resident species. Insect food is likely to be abundant in the short rains but there is no proportionate peak, except in *P. pristoptera*, where the short rains are apparently preferred.

Dicruridae Drongos

Dicrurus ludwigii Square-tailed Drongo M-P&G 1089 Category (4) 1 record.

Region B. V. I I

Dicrurus adsimilis Drongo M-P&G 1088 Category (7) 48 records.

Breeding in the rains, especially in the pre-rains periods in Regions B and C and in the short rains in Region D. There are no records for the velvet-mantled forest form D. a. coracinus.

Oriolidae Orioles

Oriolus brachyrhynchus Western Black-headed Oriole M-P&G 1168 Category (4) 1 record.

Region B. VIII, I I

Oriolus larvatus Black-headed Oriole M-P&G 1167 Category (7) 29 records.

Mainly in the rains, with peaks in both rains in Region D.

Oriolus percivali	Montane	Oriole	M-1	P&G	1169	Cate	-
gory (4) 3 records.							
Region B. II,	I.					I	
Region D. IV	, 1 ; VI, 1					2	
Oriolus chlorocephali	us Gre	en-hea	ded	Oriol	e M	-P&C	ì

Corvidae Crows, Ravens, Piapiac

1170 (4) 1 record.

Region D. X, 1

Ptilostomus afer Piapiac M-P&G 1179 Category (3). Region A. 'nesting' XI.

Corvus splendens Indian House Crow M-P&G 1174 Category (7) 31 records.

Region E. I, 1; IX, 5; X, 22; XI, 2; XII, 1 31

This well-defined breeding season, from September to January with a marked peak in October, is of particular interest in the absence of any obvious advantages in raising young during a hot, dry period of the year. All records refer to Mombasa Island where this omnivorous scavenger is common in urban and peri-urban habitats, having been introduced within the past 30 years. It is not known whether the introduction was from Zanzibar or direct from India, nor whether it was purposeful or accidental. It is believed to have been introduced to Zanzibar from Bombay around 1900, and it most likely reached Mombasa from Zanzibar.

Moreau (1950) discussed the breeding seasons (October-January) of this species and the similarly introduced Indian race of the House Sparrow Passer domesticus on Zanzibar Island (in Region D). Both species breed in Bombay April-June, in the hot weather at the beginning of the monsoon rains, and the Zanzibar season is in the short rains and the beginning of the subsequent hot weather. April-June is a cool, wet period in Zanzibar, and Moreau has noted that these breeding seasons avoid cool weather and coincide with lengthening daylight in both Zanzibar and Bombay. It is surprising that these two introduced species have shifted their Indian breeding seasons by about six months in an area of comparatively equable climate; especially when the ancestral breeding season coincides with a wet period in Zanzibar, with considerable breeding of other species (Table 12 in Moreau 1950). An introduced estrildid from south-east Asia, the Java Sparrow Lonchura oryzivora, breeds on Zanzibar Island May-August, a season coinciding with the long rains, which is a pattern typical of estrildids in East Africa (see below).

It is likely that Mombasa birds originate from Zanzibar and that they have retained their already altered breeding season. These months are dry and hot in Mombasa but follow the prolonged rains characteristic of coastal Kenya. The success of this species in and around Mombasa in recent years is testimony to the suitability of this breeding season for a scavenger.

Corvus albus Pied Crow M-P&G 1172 Category (8) 55 records.

Most records are from Regions B and D where seasons are ill-defined except for a Region D peak in and before the short rains (15/19 records October-December). Region C records are mainly in the early rains and pre-rains, as is the case elsewhere in the southern tropics (Benson 1963).

Corvus ruficollis Brown-necked Raven M-P&G 1171 Category (4) 1 record.

Region D. IV, I I

Corvus capensis Cape Rook M-P&G 1173 Category (6) 18 records.

Breeding in Region D is mainly in the rains, especially the short rains. Though associated with man to the extent that it has increased and spread with the advent of large-scale farming in Kenya's Rift Valley, nest sites are usually in acacia trees and it avoids urban areas. Unlike C. albus and C. splendens it is not prone to scavenging and is mainly insectivorous, which probably accounts for breeding peaks in both rains when insects are abundant.

Corvus rhipidurus Fan-tailed Raven M-P&G 1177 Category (4) 1 record.

Region A. VI, I I

Most records are for dry months, apart from the November records for Region D.

Paridae Tits

Parus leucomelas Black Tit M-P&G 1154 Category (4) 3 records.

Parus albiventris White-bellied Tit M-P&G 1155 Category (7) 21 records.

Region D records are spread through all months except October, with more than a single monthly record in only

March-May (8/18) and December-January (4/18). Inadequate data, but indicative of breeding mainly in the rains in both regions, with scattered records at other times. Parus funereus Dusky Tit M-P&G 1157 Category (4) 2 records.	Turdoides jardinei Arrow-marked Babbler M-P&G 725 Category (6) 12 records. Region C. II, 1; V, 1; IX, 1; X, 2; XI, 2; XII, 2 9 Region D. III, 1; V, 1 2 Region E. IV, 1 1
Region B. II, 1; XII, 1	Mainly in the rains or pre-rains. Turdoides squamulatus Scaly Babbler M-P&G 724
Category (4) I record. Region B. XII, I	Category (4) I record. Region D. IV, I I
Parus fringillinus Red-throated Tit M-P&G 1159 Category (5) 8 records. Region C. II, 1; VIII, 1	Turdoides melanops Black-lored Babbler M-P&G 726 Category (7) 41 records. Region A. IV, 3
Parus rufiventris Cinnamon-breasted Tit M-P&G 1158 Category (4) 1 record. Region C. XI, 1	Region C. III, 1; IV, 1
exhibit no clear pattern, with 7/12 records in dry months.	rains in September. Breeding in other regions is in the rains.
Remizidae Penduline Tits Remiz caroli African Penduline Tit M-P&G 1160 Category (5) 9 records. Region A. XII, I	Turdoides tenebrosus Dusky Babbler M-P&G 727 Category (4) 5 records. Region A. II, I; III, 2; IV, I; VI, I . 5 Turdoides hypoleucus Northern Pied Babbler M-P&G 729 Category (7) 22 records. Region D. II, 2; III, 2; IV, 4; V, 4; VII, I; IX, 3; X, 2; XI, 3; XII, I 22 Ill-defined breeding seasons with records in all months
SalpornithidaeSpotted CreepersSalpornis spilonotaSpotted Creeper M-P&G 1283Category (4) 2 records.Region A. XII, I	except January, June and August, but peaking in the rains April-May and November. Other <i>Turdoides</i> spp. have more clearly defined breeding seasons, mainly in the rains; the seven records in the dry months September-October and February are surprising.
Timaliidae Babblers Trichastoma fulvescens Category (4) I record. Region B. V, I	Turdoides hindei Hinde's Pied Babbler M-P&G 730 Category (4) 3 records. Region D. IV, 2; IX, I
Trichastoma pyrrhoptera Mountain Illadopsis M-P&G 738 Category (4) 2 records. Region B. V, 2	Category (6) 13 records. Region D. II, 1; III, 3; IV, 1; VI, 1; VIII, 1 7 Region E. V, 2; VI, 1; IX, 1; XI, 1; XII, 1 6 Ill-defined breeding seasons.
Trichastoma rufipennis Pale-breasted Illadopsis M-P&G 736 Category (4) 3 records. Region B. II, 1; V, 1; XII, 1 3 These few illadopsis records are mainly in the rains.	Campephagidae Cuckoo Shrikes Coracina caesia Grey Cuckoo Shrike M-P&G 1086 Category (5) 7 records. Region A. III, 1; VIII, 1; X, 1 3
Turdoides plebejus Brown Babbler M-P&G 723 Category (4) 4 records. Region A. III, I	Region B. I, 2

Campephaga quiscalina Purple-throated Cuckoo Shrike M-P&G 1084 Category (4) 2 records.

Region A. VI, 1; XII, 1

Campephaga phoenicea Black Cuckoo Shrike M-P&G 1081, 1083 Category (6) 12 records.

This woodland or forest-edge species breeds mainly in the rains (long and short).

Pycnonotidae Bulbuls

Pynonotus barbatus Common Bulbul M-P&G 741, 742, 743 Category (9) 405 records.

There are records for all months in Region D and for all but one in Regions B and C. Virtually all Region A, B and E records are in the rains, with peaks in both rains in region B, and 19/34 Region C records are October-November, in the hot pre-rains and early rains. 155/283 Region D records are from Arusha, 17 are from elsewhere in Tanzania, and 111 are from Kenya. The vast majority (125/151) of October-February records, and only 40/109 March-May records, are from Tanzania. The short rains and the subsequent between-rains period are evidently important for breeding in north-eastern Tanzania, but a significant bias has resulted from Beesley's exceptional activity prior to his departure from Arusha National Park in April 1972 (122/144 of his Pycnonotus nests were found between October 1971 and April 1972, 88 of them January-April). Kenya records peak in the long rains, in March (15), April (30), May (21), June (10) and July (8), with a hardly discernible short rains peak (six records in each of the months October, November, January and February, and single records in other months). Van Someren's data from Karen in the long rains of 1940, 1941 and 1942 represent another bias however, with all forty of his study plot nests found March-July, and no nests looked for in other months.

This ubiquitous non-forest species is the only pycnonotid for which there are more than thirty records. Most pycnonotids are forest species and most eat mainly fruit and berries. Several of the species that follow are shown to be rains breeders. Though there are many exceptions, and eggs may be laid in all or most months in many areas, the breeding of this species is often linked with the rains; especially just before and early in the rains in Regions B and C; in the short rains and the subsequent dry season in parts of Region D; in the long rains in other parts of Region D; and in the prolonged rains in Region E.

Andropadus curvirostris Cameroon Sombre Greenbul M-P&G 774 Category (4) 4 records.

Region B. IV, 2; VII, 2 4

Andropadus gracilirostris Slender-billed Greenbul M-P&G 771 Category (3).

Region B. building on 19.II.

Andropadus importunus Zanzibar Sombre Greenbul M-P&G 773 Category (7) 29 records.

Region D. I, 1; III, 2; V, 2; VIII, 1 . 6
Region E. IV, 3; V, 9; VI, 2; VII, 1; VIII, 1;
IX, 1; X, 3; XII, 3 23

Region E records peak April-May, but there are secondary peaks in the hot dry months of October and December. This is an ubiquitous non-forest species on the Kenya coast with similar ecology to *Pycnonotus barbatus* except that it favours thicker vegetation. Its breeding season is apparently less defined than that of *P. barbatus* in Region E, though the records for the latter are few.

Andropadus virens Little Greenbul M-P&G 775 Category (6) 11 records.

Andropadus latirostris Yellow-whiskered Greenbul M-P&G 776 Category (7) 26 records.

Seasons are rather ill-defined except in Region D where 8/11 records are April-June in the long rains.

Andropadus masukuensis Shelley's Greenbul M-P&G 768 Category (6) 14 records.

All August records are from Amani. Eggs were laid in all seven nests in the last week of August 1944, though all other Amani eggs were laid November-February (Moreau 1950).

Andropadus tephrolaemus Mountain Greenbul M-P&G	Phyllastrephus terrestris Brownbul M-P&G 753 Cate-
765,766 Category (7) 22 records.	gory (4) 2 records.
Region A. XI, I I	Region D. I, I I
Region B. I, I; III, I 2	Region E. VIII, I I
Region C. IX, 1; X, 1; XI, 1; XII, 1 . 4	
Region D. I, 2; II, 5; III, 1; IX, 2; X, 2;	Phyllastrephus fischeri Fischer's Greenbul M-P&G
XI, 1; XII, 2	758 Category (4) 2 records.
Though records are few, they indicate that the breeding	Region E. IV, 2
season of this highland forest species in Region D begins	
before the short rains and continues through these rains	Phyllastrephus placidus Placid Greenbul M-P&G 758
and the following between-rains period, with a February	Category (6) 17 records.
peak before the long rains.	Region C. I, I
Discussing breeding seasons on Mt Elgon in region A,	Region D. I, 1; II, 1; III, 1; IV, 5; V, 3;
Britton & Sugg (1973) suggested that species character-	VI,3; VII, 1; XII, 1
istic of forest and bamboo at high altitudes avoid breeding	This forest species breeds mainly in the rains, with
in the wettest months which are cold and misty. They	11/16 Region D records April-June and the only Region
concluded that most egg-laying is November-January,	C record in the rains.
following the rains; Betts (1966) considered September-	
December the main season on the Mau ridge at similar	Phyllastrephus albigularis White-throated Greenbul
altitudes (2500–3000 m), also in Region A. High altitude	M-P&G 761 Category (4) 4 records.
forest species breeding in Regions B and D are likely to	Region B. III, 2; IV, 1; V, 1
avoid the long rains and breed in and around the less	Region D. 111, 2, 1 v, 1, v, 1
heavy and less prolonged short rains. Montane grassland	Phyllastrephus flavostriatus Yellow-streaked Greenbul
is a less equable environment than forest or bamboo so that	M-P&G 755, 756 Category (4) 5 records.
species like Macronyx sharpei and Cisticola tinniens breed	D I O TITTY
•	
in the rains, as would congeners at lower altitudes.	Region D. I, 1; X, 1; XI, 1; XII, 1 4
	Phyllastrephus debilis Tiny Greenbul M-P&G 757
Andropadus milanjensis Stripe-cheeked Greenbul	Category (4) 2 records.
M-P&G 767 Category (4) 4 records.	
Region C. VII, I I	
Region D. I, 1; II, 1; XII, 1 3	Region E. V, I I
	Bleda syndactyla Bristlebill M-P&G 766 Category (5)
Baeopogon indicator Honeyguide Greenbul M-P&G	6 records.
751 Category (3).	Region B. IV, 3; V, 2; VIII, 1 6
Region B. building 7.III.	Few records but strongly indicative of long rains breeding.
	a the results of the state of t
Chlorocichla flaviventris Yellow-bellied Greenbul	Criniger calurus Red-tailed Greenbul M-P&G 745
M-P&G 769 Category (6) 19 records.	Category (4) I record.
Region C. I, 1; X, 1; XI, 5; XII, 1 8	Region B. VI, 1
Region D. III, 1; IV, 1; V, 1; VI, 1; XII,1 5	
Region E. V, 1; VII, 4; VIII, 1 6	Nicator chloris Nicator M-P&G 1148 Category (5) 7
Typically a bird of forest undergrowth and thicket with	
breeding seasons in the rains. Region D records are in	records.
both rains, Region C records peak in the early rains, and	Region B. IV, 2; VI, 1; VII, 1 4 Region D. XI, 1; XII, 1 2
Region E records peak after the wettest months of May-	
June, in a period of reliable and regular rainfall which	Region E. VI, I I
lacks the monsoon downpours of the preceding months.	These few records are all in the rains.
iacks the monsoon downpours of the preceding months.	Total de Thomas Wil Chate
	Turdidae Thrushes, Wheatears, Chats
Chlorocichla flavicollis Yellow-throated Leaflove	Saxicola torquata Stonechat M-P&G 882 Category (8)
M-P&G 749 Category (7) 31 records.	79 records.
Region B. I, 3; II, 1; III, 5; IV, 5; V, 4;	Region A. III, 5; IV, 11; V, 5; VI, 2 23
VI, 4; VIII, 1; IX, 1; XII, 7	Region B. II 1; IV, 1
The breeding seasons of this species are difficult to	Region C. VIII, 1; IX, 1; X, 3; XI, 3; XII, 1 9
evaluate as there are both long rains and dry season peaks,	Region D. I, 3; II, 5; III, 3; IV, 10; V, 3;
with 18/31 records March-June and 10/31 December-	VI, 3; VII, 1; VIII, 1; IX, 2; X, 3; XI, 6;
Ianuary	XII. 5

January.

XII, 5 45

Breeding is confined to the first half of the rains in Region A and the early rains and pre-rains in Region C. Region D records are for all months but they peak in both rains. The bulk of September-January records are from Arusha where breeding is in and around the short rains. Three of the February records and all of the March-August records are from Kenya where breeding is mainly in the long rains. This is an insectivorous grassland species which generally nests in sheltered sites in or under a tuft of grass or under a rock. Food and suitable nest-sites are likely to be most available when grass has begun to grow after the first rain.

Oenanthe lugens Schalow's Wheatear M-P&G 863 Category (6) 20 records.

Region D. I, 1; II, 2; III, 6; IV, 2; V, 2; VI, 2; VII, 1; X, 2; XI, 1; XII, 1 . . . 20

There are records for all months except August-September, and the breeding seasons are ill-defined apart from a peak in March at the beginning of the long rains. This is typically a species of boulderstrewn slopes in Kenya's Rift Valley, nesting in a deep crevice in rocks or walls. This specialized habitat strikes the casual observer as lacking in insect life during dry periods, but the broken, irregular ground surface probably provides haven for an equally specialized invertebrate fauna so that food is reasonably plentiful at all times.

Oenanthe pileata Capped Wheatear M-P&G 868 Category (6) 13 records.

These few records suggest that breeding is at the end of the rains and in the dry season in Region C, and mainly in the rains in Region D. This situation resembles that found in the larks Eremopterix leucopareia and Calandrella cinerea (see under E. leucotis). This wheatear, C.cinerea and Mirafra nigricans are the only southern tropics intra-African migrants which travel to higher latitudes to moult, rather than migrating southwards to higher latitudes to breed (Moreau 1966). All fourteen breeding records in Zambia are late in the dry season, between July and October (Benson et al. 1971). As in Zambia it is probably a dry season visitor to much of Region C, in the same climatic zone, but it is believed to be resident in the Kenya highlands in Regions A and D (Jackson 1938).

Cercomela familiaris Red-tailed Chat M-P&G 871 Category (4) 1 record.

Cercomela sordida Hill Chat M-P&G 873 Category (5) 9 records.

Region D. I, 3; VI, 1; VIII, 3; IX, 2

A montane moorland species which breeds mainly in the dry months following both rains. Myrmecocichla aethiops Anteater Chat M-P&G 881 Category (7) 26 records.

A hole-nesting species characteristic of open country in the highlands. 19/20 Region D records are in the rains March-July and November-December, and Region A records are in the early rains. All Region C records are from Narok where F.N. Betts (in MS) found it breeding mainly in the rains whenever they occur. Flooding of nest holes is evidently not a problem.

Myrmecocichla nigra Sooty Chat M-P&G 880 Category (7) 29 records.

A bird of short grass plains with ant-hills and scattered bush which nests and roosts in a tunnel up to 1 m long. The breeding seasons are ill-defined but there are peaks in the wet months of May and November. When bored by the birds themselves the tunnel almost invariably slopes upwards (Jackson 1938), which presumably prevents flooding or waterlogging.

Thannolaea arnoti White-headed Black Chat M-P&G 879 Category (4) records.

Region C. I, 1; VII, 1; IX, 1; X,1 . . . 4

Thamnolaea cinnamomeiventris Cliff Chat M-P&G 876 Category (6) 13 records.

Virtually all breeding is in the rains.

Monticola rufocinerea Little Rock Thrush M-P&G 853 Category (4) 3 records.

All three records are in the rains.

Cercotrichas leucophrys Red-backed Scrub Robin M-P&G 910, 911 Category (8) 53 records.

Region D. I, 1; IV, 9; V, 11, VI, 5; XII, 4 . 30 Region E. VIII, 1; X, 1; XII, 1 . . . 3

Most records are in the rains, with 12/14 Region C records November–February and 25/30 Region D records April–June.

Cercotrichas hartlaubi Brown-backed Scrub Robin M-P&G 914 Category (5) 8 records. Region B. II, 1; VIII, 1
Diceding in the rains in Region D.
Cercotrichas quadrivirgata Eastern Bearded Scrub Robin M-P&G 913 Category (4) 3 records. Region E. I, 1; XII, 2
0
Cichladusa guttata Spotted Morning Thrush M-P&G 909 Category (7) 38 records. Region A. III, 7; IV, 4; VI, 1; VIII, 1 . 13 Region B. V, 1
Region E. IV, I
Apart from two Region D records in February, all
records are in the rains.
The Morning Thrush C. arquata is retained in category
2, though there are early indefinite records from Dar es Salaam (see Jackson 1938).
Salaani (see Jackson 1930).
Alethe diademata Fire-crested Alethe M-P&G 901 Category (4) 1 record. Region B. III, 1
Alethe fuelleborni White-chested Alethe M-P&G 905 Category (4) I record.
Region D. XII, 1
1978).
1970).
Alethe poliocephala Brown-chested Alethe M-P&G 903 Category (4) 4 records.
Region B. IV, 1; V, 1; IX, 1 3
Region D. X, I I
D '11'1 Olim Andril Connel Dal'
Dryocichloides anomalus Olive-flanked Ground Robin
M-P&G 895 Category (4) 4 records. Region C. VII, 1; XI, 1; XII, 2 4
Dryocichloides poliopterus Grey-winged Ground Robin
M-P&G 887 Category (4) 2 records.
Region B. IV, 1; VI, 1
1001011 21 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1
Sheppardia cyornithopsis Akalat M-P&G 899 Category
(4) 2 records.
(4) 2 records. Region C. XII, 1
(4) 2 records. Region C. XII, I I Region D. X, I I
(4) 2 records. Region C. XII, I
(4) 2 records. Region C. XII, I
(4) 2 records. Region C. XII, I
(4) 2 records. Region C. XII, I

Sheppardia gunningi East Coast Akalat M-P&G 896 Category (3).

Region E. A young bird with adults on 1.IV, indicative of dry season breeding (see also Cercotrichas quadrivirgata).

Stiphrornis erythrothorax Forest Robin M-P&G 900 Category (4) 2 records.

Most records of these nine forest turdids are for the rains but a few are for late in the dry season, and in Region D the short rains may be preferred.

 Pogonocichla
 stellata
 White-starred
 Forest
 Robin

 M-P&G 915
 Category (7) 49 records.
 Region A. I, I; II, I; VI, I; VIII, I; IX, 2;
 X, 3.
 9

 Region B. I, I; XII, I
 2
 2

 Region C. I, 2; II, 3; V, I; X, I; XII, 3
 10

 Region D. I, I; II, 4; III, 2; IV, 5; V, 3;
 VI, I; VII, 2; VIII, I; IX, 2; X, 2; XI, 2;

 XII, 3
 2

Region A and B records are from above 2500 m and are mainly in the hot, dry months, whereas Region C records from much lower altitude are mainly in the rains. Region D breeding seasons are ill-defined with records in all months, peaking in the wet months of April, May and December, and the dry month of February. The two high altitude Mt Kenya and Aberdares records are in the dry months of September and February respectively. 14/28 Region D records are unbiassed post-1961 data from Karen (below 2000 m) February-October, with more than one record in only April (3), May (2), July (2) and September (2). Rains breeding is avoided at high altitudes, but at lower altitudes it breeds both in dry and wet seasons, preferring wet.

Cossypha natalensis Red-capped Robin Chat M-P&G 890 Category (5) 6 records.

Cossypha caffra Robin Chat M-P&G 893 Category (8) 85 records.

Most records are from Region D where they are spread over all months, but with a pronounced peak in the long rains and a small secondary peak in the short rains. Unbiassed data from the vicinity of Nairobi (only 4/48 are from the biassed Karen study) account for 35/43 March-May records, but there are Nairobi records for all months except August. The seasons are ill-defined in other regions.

Cossypha semirufa Rüppell's Robin Chat M-P&G 885 Category (7) 29 records. Region D. III, 4; IV, 9; V, 13; VI, 2; XII, 1 29

All records are in the rains; mainly in the long rains with a pronounced peak March-May (see previous species). Only three records are from the biassed Karen study. There appears to be virtually no breeding in the short rains.

Cossypha henglini White-browed Robin Chat M-P&G 884 Category (8) 67 records.

Breeding is virtually confined to the rains in Regions C and D, with marked peaks November-February (14/16 records) and April-May (19/24 records) respectively. 8/24 Region D records are from the biassed Karen study, 6/8 April-May. Region B seasons are ill-defined, though 10/27 records are April-May in the long rains.

Cossypha niveicapilla Snowy-headed Robin Chat M-P&G 892 Category (6) 20 records.

Neocossyphus rufus Red-tailed Ant Thrush M-P&G 848 Category (4) 2 records.

Stizorhina fraseri Rufous Thrush M-P&G 810 Category (4) 4 records.

Region B. IV, 3; IX, 1 4

Turdus pelios African Thrush M-P&G 840 Category (9) 151 records.

106/151 are Pitman's Uganda records and only one is from Kenya, in April. Records are spread over all months, but they exhibit a clear December-May season, with a marked peak in March at the beginning of the long rains. There is little breeding June-November and little evidence of a short rains peak. A season spanning the wettest and driest months of the year is curious, but might be explained by its predilection for fruit (as well as insects). Like the similarly sized fruit-eating starling Lamprotornis splendidus, which has a similar laying peak in March, most records are from the environs of Entebbe.

Turdus abyssinicus Nor:hern Olive Thrush M-P&G 841, 842 Category (8) 71 records.

Most records are from region D, in all months, peaking March-June (33/57). Thirty-eight unbiassed records from below 2000 m in the vicinity of Nairobi are spread over all months except August and December, peaking March-June (27) and October (4). Twelve records from Region D localities above 2200 m are December-April and September, with the greatest number in September (3). Most breeding at lower altitudes is in the long rains with virtually no short rains breeding; whereas the few records from higher altitudes suggest that the long rains are mainly avoided for breeding, with most breeding in dry or moderately wet months. Region A records are mainly in the early rains, but there is some breeding October-December; all three records away from Mt Elgon and Mau are from lower altitudes at Kitale in April.

Despite the evidence of a male in breeding condition on Rwenzori in early December, Chapin (1953) doubted the existence of any definite short nesting season. The single Region B record of an adult feeding a fledgling on Mihunga Ridge provides evidence of breeding at this season, after the short rains. A partial separation of breeding seasons by altitude is likely in highland species which breed both at high altitudes on mountains and at moderately high altitudes, more liable to severe drying out, such as the forests around Nairobi.

Turdus tephronotus Bare-eyed Thrush M-P&G 843 Category (5) 9 records.

Turdus libonyanus Kurrichane Thrush M-P&G 839 Category (4) 5 records.

Region C. IX, 1; X, 1; XI, 3 . . . 5

Turdus litsipsirupa Ground-scraper Thrush M-P&G 847 Category (4) 4 records.

Category (4) 4 records.

Region C. VIII, 1; X, 1; XI, 1; XII, 1 . . 4

The few records for this and the previous species conform with the well-established pre-rains and early rains pattern for thrushes in the southern tropics (Benson 1963).

Turdus piaggiae Abyssinian Ground Thrush M-P&G 845 Category (5) 7 records.

Region A records for this high altitude forest species are all from above 2750 m yet, surprisingly, they are all in the early rains.

Sylviidae Warblers

Bradypterus baboecala Little Rush Warbler M-P&G 948 Category (4) 5 records.

Region D. IV, 1; VI, 2; VII, 1; XI, 1 . 5
These few records are in the rains.

Bradypterus barratti Evergreen Forest Warbler M-P&G 953, 954 Category (3).

Region D. VII-X and XI-I in Mackworth-Praed & Grant (1960).

Bradypterus cinnamomeus Cinnamon Bracken Warbler M-P&G 952 Category (4) 5 records.

The few records available, from forest undergrowth at high altitudes on Mt Kenya, Mau and Kinangop, indicate that this is a dry weather breeder.

Schoenicola platyura Fan-tailed Warbler M-P&G 969 Category (5) 7 records.

Region B. II, 1; III, 1; VI, 1 . . . 3
Region D. I, 1; V, 2; X, 1 4

Acrocephalus baeticatus African Reed Warbler M-P&G 946 Category (4) 1 record.

Region C. III, I I

Acrocephalus rufescens Greater Swamp Warbler M-P&G 955, 956 Category (5) 7 records.

Region B. III, 3; IV, 1; X, 1; XI, 1; XII, 1 . 7

Acrocephalus gracilirostris Lesser Swamp Warbler M-P&G 955, 956, 957 Category (8) 66 records.

Breeding is mainly in the rains, with a pronounced long rains peak in Region D in May and a May-August peak in Region B, late in the long rains and extending into the drier months July-August. There are no region B records in the driest months January-February and only a single December record.

This species is uncommon in swamps in Region B, though it is often abundant on rocky islets in Lake Victoria where there is luxuriant herbage like Herminiera, Convolvulus and Leonotis, but no swamp. Breeding in herbage is likely to be delayed until rain has promoted plant growth, whereas breeding sites in Region D are invariably in Typha or papyrus in perennial swamps, where food supply is likely to be the ultimate factor initiating breeding. This habitat difference might account for the late breeding peak in Region B. A. rufescens is an inhabitant of papyrus swamps in Region B, and its March breeding peak at the beginning of the long rains is noteworthy. Despite the impression that perennial swamps hold abundant insect

life at all seasons, seasonality in breeding and moult is often clearly defined (Britton 1978).

Chloropeta natalensis Yellow Warbler M-P&G 805 Category (7) 22 records.

All breeding is in the rains with no breeding in the short rains. 14/19 Region D records are from the vicinity of Nairobi March-June (only two of them from the biassed

Karen study) and the remainder are from Arusha April-May.

Chloropeta similis Mountain Yellow Warbler M-P&G 806 Category (4) 3 records.

Region D. VII, 1; VIII, 1; XI, 1 . . . 3

Sphenoeacus mentalis Moustached Warbler M-P&G 1051 Category (7) 26 records.

Seasons are rather ill-defined, peaking in the long rains.

Phylloscopus ruficapilla Yellow-throated Woodland Warbler M-P&G 963 Category (4) 2 records.

Phylloscopus umbrovirens Brown Woodland Warbler M-P&G 964 Category (6) 11 records.

Region D. I, 1; VII, 1; IX, 1; XI, 1 . . 4 All localities are at high altitudes, above 2400 m, and the absence of April–June records is indicative of dry season breeding. Belcher (1941) considered it a dry season

season breeding. Belcher (1941) considered it a dry season breeder on the South Kinangop Plateau, with most breeding in January and July, but only three of his records are included here, in Region D in January, July and September.

Phylloscopus budongoensis Uganda Woodland Warbler M-P&G 965 Category (4) 1 record.

Cisticola erythrops Red-faced Cisticola M-P&G 1032 Category (7) 32 records.

Breeding is virtually confined to the long rains or just after.

Cisticola cantans Singing Cisticola M-P&G 1031 Category (9) 113 records. Region C. I, 1	Region D. I, 1; III, 6; IV, 16; V, 6; VI, 5; XI, 2; XII, 2 38 Rains breeding throughout, with a very marked long rains peak in Region D.
VI, 19; VII, 4; X, 1; XI, 5; XII, 2 . 112 96/112 Region D records are March-June in the long rains. This peak is exaggerated by biassed Karen data, in March (7), April (10), May (20), June (11) and July (1), but March-June is nevertheless a real peak, accounting for 48/63 unbiassed records.	Cisticola lais Wailing Cisticola M-P&G 1022 Category (4) 5 records. Region C. II, 1; XI, 1; XII, 1
Cisticola woosnami Trilling Cisticola M-P&G 1026 Category (7) 27 records. Region B. IV, I	Cisticola njombe Churring Cisticola M-P&G 1023 Category (4) 3 records. Region C. I, 1; II, 1; XII, 1
Well-defined rains breeding in Region C in December-March.	Cisticola galactotes Winding Cisticola M-P&G 1033 Category (8) 99 records.
Cisticola lateralis Whistling Cisticola M-P&G 1025 Category (5) 8 records. Region A. III, 1; VI, 1	Region B. II, 1; III, 2; IV, 1; V, 5; VI, 14; VII, 4; VIII, 1; X, 1; XI, 2 31 Region C. I, 4, II, 6; III, 3; IV, 1 14 Region D. I, 1; IV, 5; V, 3; VI, 2, VIII, 1; X, 1; XI, 1; XII, 2
Cisticola hunteri Hunter's Cisticola M-P&G 1030 Category (7) 45 records. Region A. I, 1; III, 1; IV, 2; IX, 1; X, 2; XI, 1 8 Region D. I, 2; III, 1; IV, 7; V, 7; VI, 8; VII, 5; IX, 2; X, 1; XI, 2; XII, 2 37 There are Region D records in all months except February and August, peaking in the long rains April-July (27/37), and with no discernible short rains peak. Thirteen April-July records are biassed, but 14/23 unbiassed records are April-July. Seasons appear to be ill-defined in Region A.	Region E. IV, 3; V, 13; VI, 8; VII, 11; VIII, 3
Cisticola chubbi Chubb's Cisticola M-P&G 1028, 1029 Category (6) 17 records. Region A. IV, 1; V, 2; VII, 2; IX, 2 . 7 Region B. I, 1; IV, 1; V, 1 3 Region C. I, 3; II, 1; XII, 1; XII, 2 7	Casticola carruthersi Carruthers' Cisticola M-P&G 1034 Category (4) 5 records. Region B. IV, 2; VI, 1; VII, 2 5 These few records are indicative of a prolonged long rains breeding season.
The breeding of the race <i>nigriloris</i> is confined to the rains (in Region C), but nominate <i>chubbi</i> has ill-defined breeding seasons in Regions A and B.	Cisticola tinniens Tinkling Cisticola M-P&G 1044 Category (6) 14 records. Region A. I, 1; VI, 1
Cisticola aberrans Rock-loving Cisticola M-P&G 1027 Category (5) 6 records. Region C. I, 1; II, 2; III, 3 6 These few records are all in the mid to late rains. Cisticola chiniana Rattling Cisticola M-P&G 1024 Category (8) 72 records. Region A. VIII, 1; IX, 1 2 Region B. III, 3; IV, 2; V, 3; VI, 2; VII, 2; IX, 1; XII, 1	VII, I

Cisticola aberdare Aberdare Cisticola M-P&G 1035
Category (6) 11 records.
Region A. I, 2; IV, 3; V, 1; VIII, 2; IX, 1;
X, 1; XI, 1
Ill-defined breeding seasons.
Cisticola robusta Stout Cisticola M-P&G 1035 Category
(7) 50 records.
Region A. IV, 1; V, 1; VI, 1; VII, 1 . 4
Region B. IV, 1; V, 1; VII, 1; X, 1; XII, 1 5
Region D. I, 1; III, 2; IV, 11; V, 10; VI, 3;
VII, 4; IX, 1; X, 3; XI, 4; XII, 2 41
Mainly in the rains, especially the long rains in Region
D, where 21/41 records are April-May.
Cisticola natalensis Croaking Cisticola M-P&G 1036
Category (7) 32 records.
Region B. IV, 2; V, 7; VI, 6; VII, 1; IX, 1;
X, I
Region C. I. 2; II, 1; XII, 3 6 Region D. III, 6; V, 2 8
Region D. III, 6; V, 2 8 Breeding is virtually confined to the rains with little
or no evidence of short rains breeding.
Cisticola cinereola Ashy Cisticola M-P&G 1042
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record.
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record. Region D. V, 1
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record.
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record. Region D. V, 1
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record. Region D. V, 1
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record. Region D. V, 1
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record. Region D. V, 1
Cisticola cinereola Ashy Cisticola M-P&G 1042 Category (4) 1 record. Region D. V, 1

Cisticola nana Tiny Cisticola M-P&G 1041 Category (5) 6 records.

Region D. I, 1; IV, 1; V, 4 6

The five April-May records are from a single visit to Mwatate (Lynes 1930).

Cisticola brachyptera Siffling Cisticola M-P&G 1037 Category (7) 21 records.

Mainly in the rains, though at the end of the prolonged rains in Region E.

Cisticola juncidis Zitting Cisticola M-P&G 1016 Category (6) 19 records.

Region B. IV, 2; VII, 2; VIII, 1 . . . 5
Region C. I, 2; III, 1; V, 1; VI, 1 . . . 5
Region D. I, 1; II, 1; V, 2; VI, 2; X, 2; XI, 1; 9

These few records suggest that breeding seasons are less clearly defined than in other cisticolas.

Cisticola aridula Desert Cisticola M-P&G 1018 Category (6) 16 records.

Breeding is mainly in the rains, with 12/14 Region D records March-June, peaking in May.

Cisticola brunnescens Pectoral-patch Cisticola M-P&G 1020 Category (7) 23 records.

Breeding is mainly in the rains, with 16/20 Region D records April-June.

Cisticola ayresii Wing-snapping Cisticola M-P&G 1019 Category (6) 12 records.

Breeding mainly in the rains, with only a single November record in Region A outside the rains, and no evidence of short rains breeding.

In many Cisticola species breeding appears to peak strongly in the long rains in Regions B and D, with little short rains breeding, certainly not proportionate to rainfall and vegetation growth at this warmer time of year.

Prinia subflava Tawny-flanked Prinia M-P&G 1045 Category (9) 180 records.

Despite the spread of records through all months in Region B, and all except September-October in Region D, this may be considered mainly a rains breeder throughout, with a prolonged season in Region E while grass is still long, and breeding in both rains in Regions B and D. 56/69 Region B records are in the long rains March-July, peaking rather late, and prolonged into the comparatively dry month of July. 58/76 Region D records are in the long rains March-June, and the removal of twelve biassed Karen records April-June does not significantly reduce this peak.

Prinia leucopogon White-chinned Prinia M-P&G 1048 Category (6) 13 records.	Apalis melanocephala Black-headed Apalis M-P&G 975 Category (4) 3 records.
Region B. I, I; IV, 2; V, 3; VI, 3; VII, I; VIII, I; IX, I; XII, I 13 Prolonged seasons in and after each rains, but mainly in	Region D. IV, I
the long rains April-June (8/13) records.	Spiloptila rufifrons Red-fronted Warbler M-P&G 987 Category (4) 3 records.
Prinia bairdii Banded Prinia M-P&G 1049 Category (4) 3 records.	Region D. II, 1; IV, 1; VI, 1
Region B. IX, 1; X, 2 3	Phyllolais pulchella Buff-bellied Warbler M-P&G 995 Category (4) 5 records.
Apalis thoracica Bar-throated Apalis M-P&G 970, 971 Category (6) 12 records.	Region A. V, I I Region B. I, I I
Region C. I, 5; II, 1; X, 1; XII, 3 10 Region D. II, 1; XII, 1 2 All Region C breeding is in the rains and pre-rains.	Region D. III, 1; IV, 1; V, 1
	M-P&G 991 Category (4) 4 records. Region D. I, 1; II, 2; XII, 1 4
Apalis pulchra Black-collared Apalis M-P&G 977, 978 Category (6) 11 records. Region A. XII, 1	Eminia lepida Grey-capped Warbler M-P&G 993
Region D. V, 7; VI, 1; XI, 1; XII, 1 . 10 All Region D records are from the vicinity of Nairobi	Category (7) 43 records. Region A. IV, 1; V, 1; VII, 1 3
and only two (both in May) are from the biassed Karen study. Breeding is in both rains with a pronounced long	Region B. IV, 3; V, 8; VI, 7; VII, 2; X, I . 21 Region D. III, 2; IV, 5; V, 5; VI, 1; VII, 2;
rains peak in May.	VIII, 1; IX, 1; XII, 1; XII, 1 19 Mainly in the rains throughout. 18/21 Region B records
Apalis jacksoni Black-throated Apalis M-P&G 982 Category (4) 2 records. Region B. IV, 1; VI, 1 2	are in the long rains April–June, and 10/19 Region D records are in the long rains April–May, including only two biassed Karen records.
Apalis flavida Yellow-breasted Apalis M-P&G 979,	Bathmocercus rufus Black-faced Rufous Warbler M-P&G 1053 Category (4) 3 records.
980 Category (8) 53 records. Region A. V. 1	Region A. XII, I
Region D. III, 2; IV, 7; V, 8; VI, 8; VIII, 1; IX, 8; X, 6; XI, 1 41	Camaroptera chloronota Olive-green Camaroptera M-P&G 1010 Category (4) 2 records.
All records for Regions A and C are in the rains. Region D records peak in the long rains April-June (23/41) and	Region B. V, 1; XII, 1
again in the dry months before the short rains, September-October (14/41). All of the latter are from Arusha, where	Camaroptera brachyura Grey-backed Camaroptera M-P&G 1009, 1011 Category (7) 46 records.
there is also a long rains peak May-June (4). All fifteen records from the vicinity of Nairobi are in the long rains March-June, including eight biassed Karen records.	Region A. IX, 1
Apalis porphyrolaema Chestnut-throated Apalis	VII, 2; VIII, 1 21 Region C. I, 2; II, 1; XII, 2 5 Region D. I, 2; III, 1; IV, 3; V, 1; VI, 6;
M-P&G 985, 986 Category (4) 3 records. Region A. XII, 1	VIII, 1; IX, 1; XII, 3
Region C. I, 1; XII, 1 2	•
	Rains breeding throughout. Region B records indicate a prolonged long rains season in March-July (18/21) and
Apalis cinerea Grey Apalis M-P&G 973, 974 Category (4) 3 records.	prolonged long rains season in March-July (18/21) and no short rains breeding. Region D records peak in the long rains in April and June and in the short rains in December.
	prolonged long rains season in March-July (18/21) and no short rains breeding. Region D records peak in the long
(4) 3 records. Region C. I, 1; II, 1 2	prolonged long rains season in March-July (18/21) and no short rains breeding. Region D records peak in the long rains in April and June and in the short rains in December. Four of the biassed Karen records are in June and the

Category (6) 17 records.	M-P&G 999 Category (4) 1 record.
Region C. II, 1; III, 1; IV, 2; V, 1; X, 1;	Region D. VI, I I
XI, 3; XII, 2	Crombecs appear to have rather widespread breeding
Region D. I, 1; V, 2; XI, 2; XII, 1 6	seasons. Their mode of hunting is careful searching, so
The pattern of records, October-May in Region C, and	that food may be available to them when more active
November-January and May in Region D are indicative	species cannot so easily obtain it.
of rains breeding.	
E I december of the Velley bellied Engage	Macrosphenus kretschmeri Kretschmer's Longbill
Eremonuela icteropygialis Yellow-bellied Eremonuela	M-P&G 764 Category (4) I record.
M-P&G 1003 Category (6) 14 records. Region C. IV, 3; V, 1; VI, 1; X, 1; XI, 3. 9	Region D. IV, I I
Region C. IV, 3; V, 1; VI, 1; X, 1; XI, 3 . 9 Region D. II, 1; III, 2; IV, 1 4	Parisoma boehmi Banded Parisoma M-P&G 787
Region E. VI, I	Category (4) 4 records.
Breeding seasons are ill-defined. Region C records	Region C. I, I
April-June are from Iringa, Dodoma and Narok.	Region D. I, 1; III, 1; IV, 1
	, , , , , , , , , , , , , , , , , , , ,
Eremontela flavicrissalis Yellow-vented Eremontela	Desires have Brown Princes M D&C -0
M-P&G 1004 Category (4) 1 record.	Parisoma lugens Brown Parisoma M-P&G 789
Region D. I, I	Category (4) 4 records. Region D. IV, 2; V, 1; XII, 1
	Region D. IV, 2; V, 1; XII, 1 4
Eremomela pusilla Green-backed Eremomela M-P&G	Hyliota australis Southern Hyliota M-P&G 814
1005 Category (4) 3 records.	Category (4) I record.
Region B. V, 2; VI 1 3	Region B. XII, I
Eremomela scotops Green-capped Eremomela M-P&G	Muscicapidae Flycatchers
1006 Category (3).	Muscicapa adusta Dusky Flycatcher M-P&G 781
Region C. Mackworth-Praed & Grant (1960)	Category (8) 71 records.
give X-XII.	Region A. I, 2; II, 2; III, 1; IV, 3; V, 4; VI,
	1; VII, 1; XII 1
Sylvietta leucophrys White-browed Crombec M-P&G	Region B. I, 1; II, 1; IV, 7; V, 2; VII, 2;
1002 Category (5) 9 records	VIII,2;XI,1;XII,1
Region A. III, 1; IV, 1	Region C. X, 1; XI, 1
VII, 1; XII, 1	Region D. I, 8; II, 6; III, 6; IV, 4; V, 3;
, , , , , , , , , , , , , , , , , , , ,	VI, 1; IX, 1; X, 3; XI, 3; XII, 2 37 Breeding seasons are ill-defined, but peaking in the rains
Sylvietta virens Green Crombec M-P&G 1001	in Regions A (April-May) and B (April). The large number
Category (4) 5 records.	of between-rains records from region D are only partly
Region B. II, 1; III, 1; IV, 1; V, 1; VI, 1; . 5	accounted for by records from localities above 2200 m
	(all seven January-March) and Arusha (3/7 records January-
Sylvietta brachyura Crombec M–P&G 996 Category(5)	February). Records from the vicinity of Nairobi are
7 records.	December-May, peaking March-April (7/11 records).
Region B. II, 1; III, 1; VI, 1	
Region D. I, 1; V, 2; X, 1 4	Muscicapa aquatica Swamp Flycatcher M-P&G 782
	Category (7) 26 records.
Sylvietta whytii Red-faced Crombec M-P&G 997	Region B. III, 3; IV, 3; V, 4; VI, 3; VIII, 2;
Category (7) 34 records.	IX, 1; X, 2; XI, 7
Region B. III, 2; VI, 1	Region C. VI, I I
Region C. II, 1; IV, 1; V, 1; IX, 1; X, 2	Region B records are mainly in the long rains March-
XI, 1; XII, 1 8	June (13/25) and the short rains October-November
Region D. I, 1; III, 7; IV, 2; V, 1; VI, 1;	(9/25). Such a marked short rains peak is exceptional in
IX, 2; X, 3; XI, 5; XII, I 23	Region B. This species' habit of nesting in discarded
Seasons are rather ill-defined, but there are peaks in the early rains or pre-rains in Regions B (March), C (October)	weaver nests might be expected to lead to late nesting, but late in the long rains rather than peaking in the short rains.
and D (March), and a further Region D peak in and before	If nests discarded at the end of the long rains were utilised
the short raise in October November	in the chart raine leving should be astly in the short rains

Sylvietta isabellina

Somali Long-billed Crombec

Camaroptera simplex

the short rains in October-November.

Grey Wren Warbler M-P&G 968

in the short rains, laying should be early in the short rains,

September-October rather than November. These Nov-	Region C. XII, 1
ember records are of clutches taken by Pitman in three	Breeding mainly in the rains, with 27/31 Region B
localities in three different years. There is no peak late in	records in March-June, especially in the early rains in
the long rains, but the Chestnut Sparrow Passer eminibey,	March-April.
Cut-Throat Amadina fasciata and Silverbill Lonchura	M.I. and the Constant Dist. There is
malabarica, which utilise discarded ploceid nests, exhibit	Melaenornis pammelaina Southern Black Flycatcher
such peaks in Region D in June-July (see below).	M-P&G 799 Category (4) 4 records.
Walter Could Com Florest w M DCC	Region C. X, 2
Muscicapa cassini Cassin's Grey Flycatcher M-P&G	Region D. III, 1; XI, 1 2
784 Category (4) 3 records.	English to the second of the state of the second of the se
Region B. VI, 1; VII, 1; XI, 1 3	Empidornis semipartitus Silverbird M-P&G 801 Cate-
Muscicapa lendu Chapin's Flycatcher Category (4) I	gory (6) 12 records.
record.	Region A. II, 1; V, 1
Region B. II, I I	
The nest and eggs of this little known species are still	Region C. I, 3; II, 1; XI, 1; XII, 1 6 Region D. IV, 1; V, 1; IX, 1 3
undescribed. This record is of a recently-fledged young	Region D. IV, 1; V, 1; IX, 1 3 This bush-loving species breeds in both wet and dry
bird begging from an adult.	months but all Region C records are in the rains.
ond begging from all addition	months but an Region C records are in the rams.
Muscicapa caerulescens Ashy Flycatcher M-P&G 785	Production mismalous but Do Company
Category (5) 7 records.	Bradornis microrhynchus Grey Flycatcher M-P&G
Region B. II, 1; V, 2; VI, 1; VIII, 1; IX, 1 . 6	793, 794 Category (8) 55 records.
Region E. V, I I	Region A. III, 1; V, 1
	Region B. VI, 2
Muscicapa comitata Dusky Blue Flycatcher M-P&G	1; VIII, 1; IX, 7; X, 4; XI, 3; XII, 4 . 34
803 Category (4) 2 records.	Region D. II, 1; III, 1; IV, 2; V, 2; VI, 3;
Region B. VII, 1; X, 1 2	VIII, 2; XII, 6
	Ill-defined breeding seasons, especially in Region C
	where there are records for all months except July; 2/34
Myioparus plumbeus Grey Tit Flycatcher M-P&G 788	records are June-August, in the dry season, but the greatest
Category (3).	number is for September-October, in the hot pre-rains.
Region B. building in IV.	Region D records peak in the short rains in December (6),
White and Class Discount	with a secondary peak April-June (7) in the long rains.
Melaenomis chocolatina White-eyed Slaty Flycatcher	
M-P&G 796 Category (9) 106 records. Region A. III, 1; XI, 3; XII, 4 8	Bradornis pallidus Pale Flycatcher M-P&G 792, 795
	Category (7) 27 records.
	Region A. III, 1; VIII, 1 2
Region C. IV, 1; V, 1; XII, 2 4 Region D. I, 18; II, 5; III, 5; IV, 14; V, 12;	Region B. III, 1; IV, 1; V, 2 4
VI, 3; VII, 1; VIII, 2; IX, 6; X, 9; XI,	Region C. III, I I
10; XII, 8 93	Region D. I, 1; II, 1; III, 3; IV, 3; V, 1;
36/93 Region D records are from Arusha, accounting for	X, 1; XI, 2; XII, 1
most of the records in January (12/18), September (6/6)	Region E. IV, 1; V, 1; VI, 3; VIII, 1; IX, 1. 7
and October (7/9). Records from elsewhere peak in the	Breeding is mainly in the rains, including the short
long rains in April (11/57) and May (11/57) and in the	rains in Region D.
short rains in November (10/57) and December (10/57). All	
eight Region A records are from localities above 2100 m	Megabyas flammulata Shrike Flycatcher M-P&G 811
in the dry season.	Category (4) 2 records.
	Region B. IV, 1; VI, 1 2
Melaenornis ardesiaca Yellow-eyed Black Flycatcher	•
M-P&G 799A Category (3).	Bias musicus Black & White Fylcatcher M-P&G 812
Region B. A half built nest on 10.II.	Category (6) 11 records.
	Region B. III, 3; IV, 2; V, 1; VII, 1; IX, 1 . 8
Melaenornis edolioides Black Flycatcher M-P&G 798	Region C. XI, I I
Category (7) 38 records.	Region D. I, I
Region A. III, 2; IV, 3; V, I 6	Region E. VI, I
Region B. I, 1; II, 1; III, 12; IV, 10; V, 3;	This and the previous species show a preference for
VI, 2; X, 1; XII, 1 31	rains breeding.

Batis mixta Puff-back Flycatcher M-P&G 815 Category (4) 2 records. Region E. V, 1; VI, 1 2 Both records are in the wettest months.	Erannornis longicauda Blue Flycatcher M-P&G 827 Category (7) 36 records. Region A. IV, 1; VII, 1
Batis molitor Chin-spot Puff-back Flycatcher M-P&G 817 Category (7) 38 records. Region A. IV, 1; V, 1	VIII, 1; X, 1; XII, 1 30 Region C. I, 2; VI, 1; XII, 1 4 27/30 Region B records are in the long rains March-July, especially March-May.
XII, 1	Trochocercus nitens Blue-headed Crested Flycatcher M-P&G 830 Category (4) 1 record. Region B. IV, 1
Pre-rains and early rains breeding in Region C. 8/18 Region D records are from Arusha October-February, including 6/8 October-November records. The few data	Trochocercus nigromitratus Dusky Crested Flycatcher M-P&G 831 Category (4) 1 record.
from elsewhere in Region D are indicative of long rains and short rains breeding.	Region B. IX, I I
Batis soror East Coast Puff-back Flycatcher M-P&G 817 Category (4) 4 records.	Trochocercus albiventris White-bellied Crested Flycat- cher M-P&G 831 Category (4) 1 record.
Region D. I, I	Region B. IV, 1
Region E. I, 2; V, 1 3	
Batis minor Black-headed Puff-back Flycatcher M-P&G 820 Category (5) 6 records.	Trochocercus albonotatus White-tailed Crested Flycat- cher M-P&G 829 Category (4) 5 records.
Region A. III, I I	Region D. X, 5 5
Region B. IV, 1; V, 1	All at Amani in October 1938, before the short rains (Moreau 1950).
Region E. VI, 1; X, 1	Terpsiphone rufiventer Red-bellied Paradise Flyeatcher
though two at least of the <i>B. soror</i> records are for a very dry period (January, Region E).	M-P&G 835 Category (7) 45 records. Region B. I, 1; III, 1; IV, 18; V, 8; VI, 9;
Platysteira cyanea Wattle-eye M-P&G 822 Category	VII, 4; X, 1; XI, 2; XII, 1 45 Mainly in the rains, with 35/45 records in the long rains
(6) 13 records. Region B. II, 1; IV, 5; V, 2; VI, 2; VIII, 1; XI, 1; XII, 1	April-June, peaking in April, and very little breeding in the short rains.
Mainly in the long rains, with 9/13 records April-June.	
Platysteira peltata Black-throated Wattle-eye M-P&G	Terpsiphone viridis Paradise Flycatcher M-P&G 832, 833, 834 Category (8) 95 records.
823 Category (5) 10 records. Region A. XII, 1	Region A. III, 1; IV, 3; VI, 1; VII, 1 . 6 Region B. III, 1; IV, 2; V, 5; VI, 1; VII, 5 . 14 Region C. I, 2; III, 1; IV, 1; XI, 2; XII, 4 . 10
X, 2; XI, 2 9 Seasons are apparently ill-defined.	Region D. I, 6; II, 10; III, 3; IV, 10; V, 12; VI, 3; VII, 2; VIII, 3; IX, 2; X, 3; XI 5;
Platysteira castanea Chestnut Wattle-eye M-P&G 824	XII, 6; 65 Rains breeding in Regions A, B and C. 25/65 Region D
Category (4) 1 record. Region B. V, 1	records are from the vicinity of Nairobi, mainly in the long rains in April (9), May (7), and June (4). All October-
Platysteira blissetti Jameson's Wattle-eye M-P&G 825 Category (4) 1 rccord. Region B. VI, 1	December records and 7/10 February records are from north-eastern Tanzania at Arusha, Amani, Korogwe and Moshi. Short rains and between-rains breeding in parts
Platysteira concreta Yellow-bellied Wattle-eye M-P&G 826 Category (4) 1 record. Region B. XI, 1	of Region D and long rains breeding in other parts leads to a confusing pattern of records if this region is dealt with as a single entity. However, in any part of it one or other rainy season seems to be preferred.

Motacillidae Wagtails, Pipits, Longclaws

Motacilla capensis Cape Wagtail M-P&G 693 Category

(6) 15 records.

Region B. III, 1; VI, 1; VII, 2; VIII, 2; IX, 1; XI, 1; XII, 1 9
Region D. I, 1; IV, 1; V, 1; VII, 1; IX, 2 6

These few records indicate that breeding seasons are rather ill-defined, peaking after the long rains when water levels are high and unlikely to rise.

Motacilla clara Mountain Wagtail M-P&G 692 Category (7) 22 records.

Rains breeding in Region C but rather ill-defined elsewhere.

Motacilla aguimp African Pied Wagtail M-P&G 691 Category (9) 117 records.

Most breeding is in the rains in Regions A and C. Laying in Region B peaks in the long rains in May, and there are minor peaks before and after the short rains and before the long rains. There are records for all months in Region D, and for eleven months in Region E, where 20/22 records refer to the same site, in a boat at Watamu (Donnelly 1978). Like some hirundines it breeds in close association with human dwellings, where water and insects are likely to be available during dry periods (44/46 cards refer to buildings or boats).

Wagtails tend to have rather elastic breeding seasons with ill-defined peaks, especially *M. aguimp* which is often associated with human habitations. Watersides are likely to provide abundant food at any time, and breeding in the truly aquatic species is more likely to be limited by other factors.

Anthus novaeseelandiae Richard's Pipit M-P&G 706 Category (8) 75 records.

Region E. V, 3; VIII, I 4
Rains breeding in Regions B and E, and a pronounced peak in Region D in the long rains (April-May, 26/43 records). Dry season records in Region C are from central and southern Tanzania, with a peak of 10/17 August-September. Insects are plentiful during this hot pre-rains period (Benson 1963) and they are more readily located when grass is short, though there are fewer secure sites where nests may be hidden.

Anthus leucophrys Plain-backed Pipit M-P&G 704, 705 Category (5) 7 records.

Few records but indicative of breeding in the long rains.

Anthus melindae Malindi Pipit M-P&G 709 Category (5) 6 records.

Region E. IV, 2; V, 3; VI, 1 . . . 6 Breeding in the rains.

Anthus similis Long-billed Pipit M-P&G 703 Category (7) 22 records.

Rains breeding in Regions B and C, though prolonged into dry weather in Region B. All January-March records for Region D are from Arusha in 1972 and should not be considered necessarily typical. Kenya records are for April-May only.

Anthus brachyurus Short-tailed Pipit M-P&G 711 Category (4) 2 records.

Region C. II, I; XII, I 2

Anthus caffer Little Tawny Pipit M-P&G 712 Category (4) 3 records.

Anthus lineiventris Striped Pipit M-P&G 714 Category (4) 1 record.

Region D. XI, I I

Tmetothylacus tenellus Golden Pipit M-P&G 715 Category (4) 3 records.

The few records of this and the previous three species are indicative of rains breeding. Although pipits breed on the ground, they usually breed in the rains, the only one showing a preference for dry-season breeding being A. novaeseelandiae in Region C.

Yellow-throated Longclaw M-P&G Macronyx croceus 716 Category (9) 104 records. Region A. III, 1; IV, 2; V, 2; VI, 4; VII, 3 Region B. III, 1; IV, 11; V, 15; VI, 13; VII, 3; VIII, 1; IX, 1; X, 5; XI, 3 53 Region C. I, 2; II, 1; IV, 2; XII, 3. 8 Region D. I, 2; II, 2; III, 4; IV, 6; V, 4; VI, 3; VII, 4; IX, 1; X, 1; XI, 1 XII, 1 29 2 Region E. VIII, 2

Breeding is virtually confined to the rains in all regions, including a marked short rains peak in Region B October-November. Though there are Region D records for all months except August, 21/29 are for March-July in the long rains. Grass cover for hiding nests is likely to be very important for longclaws.

Fülleborn's Longclaw M-P&G Macronyx fuelleborni 717 Category (4) 3 records.

Region C. V. 1; XI, 1; XII 1

Macronyx sharpei Sharpe's Longclaw M-P&G 718 Category (6) 19 records.

Region A. III, 1; IV, 2; V, 4; VI, 1; IX, 1; Region D. III, 1; IV, 5; V, 2; X, 1 . . . 9

Breeding in montane grasslands above 2500 m (one at 2000 m) in the rains.

Macronyx aurantiigula Pangani Longclaw M-P&G 720 Category (6) 16 records.

> Region D. I, 2; II, 2; III, 3; IV, 2; V, 3; Region E. VII, 1 . . .

No short rains breeding, but a January-May season beginning after the short rains when grass is long.

Macronyx ameliae Rosy-breasted Longclaw M-P&G 721 Category (5) 11 records.

Region C. IV, 1; V, 1; XII, 1 . . . Region D. IV, 1, V, 5; VI, 1; XII, 1

Few records but indicative of breeding in the rains or immediately afterwards, with a pronounced Region D peak in May.

Although longclaws are ground breeders they all lay in the rains (like pipits). Where there are two rainy seasons there is a marked preference for the long rains, even in high altitude species where the long rains is the colder of the two wet seasons. In Region C records are for the rains or late in the rains when grass is long.

Bush Shrikes Malaconotidae

Nilaus afer Northern Brubru M-P&G 1098 Category (6) 15 records.

Region C. II, 1; IV, 1; V, 1; VI, 1; XI, 1 . 5 Region D. III, 4; V, 3; VIII, 1; IX, 1; X, 1 10 Most Region D records are in the long rains, though scasons are ill-defined elsewhere.

Dryoscopus priuglii Pringle's Puff-Back M-P&G 1130 Category(4) I record. Region D. XI, 1 Dryoscopus gambensis Puff-Back M-P&G 1131 Category (4) 2 records. Region A. I, 1 Region B. X, 1 Black-backed Puff-Back M-P&G Dryoscopus cubla 1128, 1129 Category (6) 19 records. Region C. I, 1; II, 1: III, 1 3 Region D. I, 1; II, 1; III, 1; IV, 4; V, 2; Region E. IX, 1; XII, 1 . . . Breeding in the rains in Region C and peaking in both

rains in Region D, though seasons in Regions D and E are probably rather ill-defined.

Dryoscopus angolensis Pink-footed Puff-Back M-P&G 1132 Category (4) 2 records.

Region B. IV, 1; VII, 1; also building in III and IV

Tchagra minuta Marsh Tchagra, M-P&G 1136 Category (5) 7 records. Region A. V, 2; VI, I . . .

Region B. III, 2; IV, 1; IX, 1 All but one of these records are in the rains.

Tchagra jamesi Three-streaked Tchagra M-P&G 1135 Category (4) 2 records.

Region E. V. 2

Tchagra australis Brown-headed Tchagra M-P&G 1134 Category (8) 54 records.

Region C. I, 3; II, 3; III, 3; IV, 1; V, 1; VI, 1; X, 1; XI, 2; XII, 6 . . . 21 Region D. I, 1; II, 3; III, 9; IV, 2; V, 3; VI, 4; VII, 2; IX, 1; X, 1; XII, 2 . . . 28 Region E. IV, I

Tchagra senegala Black-headed Tchagra M-P&G 1133 Category (8) 51 records.

> Region A. IV, 1; VI, 1; X, 1 3 Region B. II, 1; V, 2; VI, 2 . . . 5 Region C. I, 1; II, 1; IV, 1; V, 1; X, 4; XI, 2; XII, 1 Region D. I, 1; II, 2; III, 7; IV, 6; V, 2; VI, 1; X, 1; XI, 2; XII, 2 . . . 24 Region E. V, 2; VI, 1; VII, 1; VIII, 4 .

This and the previous species are mainly rains breeders, with peaks in the early rains in both Region C and D, as early as October (pre-rains) in this species in Region C.

Rhodophoneus cruentus Rosy-patched Shrike M-P&G 1147 Category (5) 6 records.

Region D. IV, 2; V, 2; VI, 1; XI, 1 . . .

Laniarius ferrugineus Tropical Boubou M-P&G 1125 Category (7) 46 records. Region A. IV, 1; VI, 1; IX, 1; X, 1. 4 Region B. III, 1; IV, 2; V, 2; VI, 3; VII, 1	
Region B. VII, I I Malaconotus nigrifrons Black-fronted Bush Sh. M-P&G 1140 Category (4) I record. Laniarius ferrugineus Tropical Boubou M-P&G 1125 Category (7) 46 records. Region A. IV, I; VI, I; IX, I; X, I	ike
Laniarius ferrugineus Tropical Boubou M-P&G 1125 Category (7) 46 records. Region A. IV, 1; VI, 1; IX, 1; X, 1	rike
Region A. IV, 1; VI, 1; IX, 1; X, 1	
Region D. I, 2; II, 3; III, 5; IV, 3; V, 5; VI, 1; VII, 3; X, 3; XII, 2	\$G
All Region B breeding is in the long rains March-July, but the pattern of Region D records is confusing, with only 13/27 March-May and the remainder spread over wet and dry months. The ten records from elsewhere are in the rains. Laniarius barbarus Black-headed Gonolek M-P&G 1119 Category (7) 41 records. Region A. III, 3; IV, 2	rike
dry months. The ten records from elsewhere are in the rains. Laniarius barbarus Black-headed Gonolek M-P&G I Category (4) 5 records. Region A. III, 3; IV, 2	
Laniarius barbarus Black-headed Gonolek M-P&G Region A. I, 1; II, 2; V, I	117
Region A. III, 3; IV, 2 5	
Region B. I, 1; III, 2; IV, 5; V, 15; VI, 7; Corvinella melanoleuca Magpie Shrike M-P&G I	
IX, 3; X, 1; XI, 1; XII, 1 36 Category (4) 3 records. Breeding early in the rains in Region A, and in the long rains in Region B, especially April–June (27/36 records), Region D. II, 1; III, 1	
peaking in May. There is virtually no October-November breeding but there are three September records at the Lanius mackinnoni Mackinnon's Shrike M-P&G I	110
beginning of the short rains. Category (6) 15 records. Region B. II, 4; III, 2; IV, 4; V, 1; VI, 2; Laniarius fuelleborni Fülleborn's Black Boubou M-P&G VII, 1; VIII, 1	
1124 Category (4) 3 records. Region C. I, I; II, I, XII, I	ong
All three records are in the rains. Lanius excubitorius Grey-backed Fiscal M-P&G I Category (8) 72 records.	102
Laniarius funebris Slate-coloured Boubou M-P&G 1121 Region A. III, 3; IV, 2; XI, 1 6 Category (6) 18 records. Region B. XI, 1	
Region C. I, I; III, I; IV, I; V, 2; X, 2; XI, I; XII, 3 Breeding records for all months except January	in
Region D. III, I; V, 2; XI, 2 · · · · 5 Region E. X, I · · · · I A prolonged October-May season in Region C, in and around the rains, and breeding in both rains in Region D. Region B and an ill-defined season in Region D, the 37/61 Region B records are March-June in the long rains of 5/6 Region A records are at the beginning of the rains of	ins
Malaconotus bocagei Grey-green Bush Shrike M-P&G Lanius cabanisi Long-tailed Fiscal M-P&G 1141 Category (4) 3 records. Category (7) 29 records.	108
Region B. II, 1; VII, 1; VIII, 1	
Malaconotus sulfureopectus Sulphur-breasted Bush Shrike M-P&G 1138 Category (4) 5 records. Region A. VI, I	s in

Lanius dorsalis Taita Fiscal M-P&G 1107 Category (5) 9 records.

Breeding in the rains. The Region C record for June is from Narok.

Lanius somalicus Somali Fiscal M-P&G 1106 Category (4) 2 records.

The arid thorn-bush habitat of this and the previous species probably accounts for the concentration of records in the wettest months when food is likely to be most plentiful. The less arid areas occupied by *L. cabanisi* are evidently less markedly seasonal, enabling breeding to take place in the driest months.

Lanius collaris Fiscal M-P&G 1104, 1105 Category (9) 246 records.

Region A. I, 1; II, 4; III, 1; IV, 8; V, 9;

Rains and pre-rains breeding in Regions A and C; long rains breeding in Region B, and records for all months except August in Region D. The wet April-May and November-December periods are especially well represented in Region D, and the between-rains months of January-March have the most records outside of these periods. 123/191 Region D records are from the vicinity of Nairobi, peaking April (17), May (29), November (23) and December (18).

Most shrikes prefer to breed in the rains but several also have records for the dry season, perhaps not surprising in species which are not purely insectivorous but also prey on young birds, reptiles etc.

Prionopidae Helmet Shrikes

Eurocephalus anguitimens White-crowned Shrike M-P&G 1097 Category (6) 15 records.

-		()					
	Region A. V, 1						I
	Region B. III, 1						I
	Region C. III, 1;	XI, 1					2
	Region D. II, 1;	Ш, і;	V, 2	; VI, r	; VII	ί, ι;	
	VIII, 1; XI, 3;	XII,	I				11

Seasons are rather ill-defined but mainly in the rains, with May and November peaks in both rains in Region D.

Prionops plumata Crested Helmet Shrike M-P&G 1090, 1091 Category (5) 6 records.

Prionops poliolopha Grey-crested Helmet Shrike M-P&G 1092 Category (4) 2 records.

Prionops retzii Retz's Red-billed Shrike M-P&G 1095 Category (4) 3 records.

Prionops scopifrons Chestnut-fronted Shrike M-P&G 1096 Category (6) 13 records.

Mainly rains breeding in Region E.

Sturnidae Starlings and Oxpeckers

Poeoptera stuhlmanni Stuhlmanni's Starling M-P&G 1209 Category (4) 4 records.

Poeoptera kenricki Kenrick's Starling M-P&G 1210 Category (6) 17 records.

Seasons are ill-defined. There is a marked peak before the short rains, though all September-November records are from Arusha.

Onycognathus walleri Waller's Chestnut-winged Starling M-P&G 1201 Category (4) 4 records.

Onycognathus morio Red-winged Starling M-P&G 1203 Category (7) 30 records.

Brown (1965a) concluded that breeding in Embu is mainly November-February, in and after the short rains, and presumably at a time when fruits (predominant in the diet of the young at Embu) and insects are most plentiful. The more comprehensive data now available confirm that the breeding season in Region D begins before the short rains in October and extends to the beginning of the long rains in March. There is a peak in the hot pre-rains period (March) but the long rains are mainly avoided.

Onycognathus temuirostris Slender-billed Chestnut-winged Starling M-P&G 1205 Category (7) 28 records.

Brown (1965a) attributed its dry season (January-March) breeding in Embu to its habit of nesting in moist sites in caves under waterfalls. Timing is evidently critical as both spate and severe drought periods are avoided. Ideally, sites should be secure throughout the incubation and fledgling period, but water levels should be at their lowest when young leave the nest, and the fledging of the young is known to be delayed if rivers are still in flood when young are mature enough to fly. The only Region D records not discussed by Brown are from Mt Kenya in August (no details) and May, the latter at Timau involving an egg laid on 27 May in a typical site under a small waterfall. This locality is part of the Mt Kenya rain-shadow area centred on Nanyuki, with April-May and August-November rains, whereas Embu is south-east of the mountain with a more typical Region D rainfall pattern. It is likely that water was high but receding at the time of laying. Region A records are from waterfalls at Mau Narok in the dry season, but Region C records all refer to young fledging during the rains at Njombe. A juvenile with a parent at Njombe in August is excluded from the tabulated data. It might have fledged when rivers were receding after

the rains.
Lamprotornis purpureiceps Purple-headed Glossy Star-
ling M–P&G 1193 Category (4) 1 record.
Region B. IV, I I
Lamprotornis corruscus Black-breasted Glossy Starling
M-P&G 1194 Category (5) 6 records.
Region D. I, 1; XI, 1; XII, 1 3
Region E. V, 1; VIII, 1; X, 1 3
Lamprotornis splendidus Splendid Glossy Starling
M-P&G 1192 Category (7) 25 records.
Region A. III, 1; IV, 2; V, 1 4
Region B. I, 1; II, 2; III, 14; IV, 1; V, 1;

Breeding early in the rains in Region A. Two-thirds of Region B records are in March, referring to clutches taken by five collectors in at least seven different years, mainly at Entebbe where it is very common. They evidently represent a real peak in breeding activity which is possibly correlated with a local abundance of fruit at the beginning of the long rains.

VII, 1; VIII, 1 21

Lamprotornis purpureus Purple Glossy Starling M-P&G
1191 Category (4) 2 records.
Region B. II, 1; IV, 1. 2

Lamprotornis chloropterus Lesser Blue-eared Glossy Starling M-P&G 1190 Category (4) 3 records.

Region B. III, 1; V, 1; VI, 1 3

Region C. I, 3; X, 2; XI, 1 . . . 6
Region D. I, 1; II, 1; III, 4; IV, 2; V, 2;
VI, 3; VII, 1; XI, 1; XII, 1 . . . 16

Breeding is early in the rains in Region A, in the prerains and rains in Region C, and mainly in the long rains March-June (11/16 records) in Region D.

Rains breeding in Regions A and C, and to a large extent in Region B, though there are more records for January than for any other month. This is the driest month when its characteristic habitat of acacia thornbush would be expected to lack food, with little chance of improvement in February when young would be fledging. The few Region D records are in the short rains or immediately beforehand.

Except in southern Tanzania this is mainly a non-breeding migrant to our area, often appearing at times of local abundance of fruits; though present long enough to breed in most areas, they apparently do not. These few records are in the early rains.

Cinnyricinclus femoralis Abbott's Starling M-P&G 1186 Category (4) 4 records.

Region D. II, 1; III, 1; X, 2 4

Cimpyricinclus sharpii Sharpe's Starling M-P&G 1185 Category (4) I record.

Scarce records for these two forest starlings suggest a preference for breeding at the end of the dry season.

Spreo fischeri Fischer's Starling M-P&G 1211 Category
(5) 8 records.

Region D. IV, 2; V, 1; IX, 1; X, 1; XI, 3 8

Spreo hildebrandti Hildebrandt's Starling M-P&G

Spreo superbus Superb Starling M-P&G 1216 Category (8) 69 records. Region A. V, 2. 2 Region C. I, 3; III, 1; VI, 1; VII, 1; IX, 1; X, 1; XI, 3; XII, 1 12 Region D. I, 3; II, 5; III, 16; IV, 8; V, 3; VI, 4; VIII, 1; IX, 2; X, 2; XI, 4; XII, 5 53 Region E. IV, 2 2 Cosmopsarus unicolar (4) 2 records. Ashy Starling M-P&G 1199 Category (4) 2 records.	Region D. I, 3; II, 4; III, 3; IV, 1; V, 1; VI, 3; VII, 1; VIII, 1; IX, 1; X, 2; XI, 3; XII, 3
Region D. II, 1; III, 1	A records are early in the rains April-May in contrast to the spread of records in Region D throughout the year.
The above six species are typically inhabitants of acacia thorn-bush in arid and semi-arid areas. Two or three	Nectariniidae Sunbirds Anthreptes fraseri Grey-headed Sunbird M-P&G 1280 Category (4) 1 record, Region B. VII, 1
imilarly sized species may be found on the same ground, uggesting that each has particular feeding preferences; but broadly speaking they are birds of similar ecology, eating mainly insects and berries. The bulk of breeding is in the rains. There are S. superbus records in Region D in ll months except July, but there are discernible rains peaks	Anthreptes reichenowi Plain-backed Sunbird M-P&G 1279 Category (5) 8 records. Region D. III, 1 Region E. IV, 1; V, 1; VII, 1; VIII, 1; IX, 1; X, 1; XI, 1 7
March-April and November-December. Shelley's Starling <i>Spreo shelleyi</i> is retained in category 2, despite the record (undated) of young birds being fed by their parents in south-eastern Kenya in van Someren (1922), which led Hall & Moreau (1970) to state that it certainly breeds in this area. We doubt that this northern species breeds within our limits; see especially the discussion of its migratory status in northern Somalia in Archer & Godman (1961).	Anthreptes rectirostris Category (4) 1 record. Region B. VIII, 1 Anthreptes rubritorques Region D. I, 1 Category (4) 1 record. Region D. I, 1 Anthreptes rubritorques Region D. I, 1 Anthreptes rubritorques Region D. I, 1
Creatophora cinerea Wattled Starling M-P&G 1182 Category (5) 8 records. Region D. IV, 1; V, 4; VII, 1; XII, 2 . 8 This species is mainly nomadic or migratory in our	Authreptes pallidigaster Category (4) I record. Region E. V, I Very N. W. Leeberg and M-P&G 1278
area, with movements and breeding closely linked with exceptionally verdant periods in arid and semi-arid areas. The few breeding records listed are in the long and short rains. Numbers are minimal as this species is intensely gregarious when breeding; full counts in each case would have involved scores of nests.	Anthreptes longuemarei Uganda Violet-backed SunhiJd M-P&G 1274 Category (4) 1 record. Region C. III, 1
Buphagus africanus Yellow-billed Oxpecker M-P&G 1217 Category (5) 9 records. Region A. IV, I; V, I	Region C. I, 2
Buphagus erythrorhynchus Red-billed Oxpecker M-P&G 1218 Category (7) 32 records. Region A. V, 1;	Anthreptes neglectus Uluguru Violet-backed Sunbird M-P&G 1275 Category (4) I record. Region D. XII, I I In addition to this record from Pugu Hills, building has been observed at Amani on 27 December.

Anthreptes collaris Collared Sunbird M-P&G 1271 Category (9) 119 records. Region A. XII, 2	Nectarinia rubescens Green-throated Sunbird M-P&G 1262 Category (5) 7 records. Region B. V. 1; VI, 2; VIII, 1; X, 1; XI, 1; XII, 1			
	and August-September. This mainly insectivorous species is undoubtedly a rains breeder in Region D, preferring the long rains.	1263 Category (9) 140 records. Region A. II, 1; III, 2; IV, 2; V, 1; VII, 1; IX, 1; X, 2		
	Anthreptes platura Pygmy Sunbird M-P&G 1236 Category (4) 2 records. Region A. X, I; XII, I 2	VI, 13; VII, 12; VIII, 1; IX, 5; X, 1; XI, 2; XII, 1		
	Nectarinia seimundi Little Green Sunbird M-P&G 1277 Category (3). Region B. building in VIII.	Region D. I, 3; II, 6; III, 10; IV, 4; V, 5; VI, 6; VII, 2; VIII, 2; IX, 3; X, 7; XI, 3; XII, 3		
	Nectarinia olivacea Olive Sunbird M-P&G 1269 Category (7) 31 records. Region B. II, 1; III, 1; IV, 1; VI, 1; IX, 1; X, 1 6 Region D. I,2; II, 2; III, 2; IX, 2; XI, 2; XII, 4 I4 Region E. IV, 3; V, 2; VI, 2; VII, 1; VIII, 2; X, 1	Region E. IV, 1; V, 1; VI, 1; VII, 1; IX, 1; X, 1		
	Nectarinia verticalis Green-headed Sunbird M-P&G 1266 Category (7) 23 records. Region B. III, 1; IV, 5; V, 2; VI, 2; VII, 5;	Nectarinia hunteri Hunter's Sunbird M-P&G 1264 Category (4) 2 records. Region D. X, 2 2		
	VIII, 3; IX, 4; X, I 23 All records of this forest species are for March-October, peaking early in the long rains in April and again July-September between the rains. Both nectar and insects are taken, mainly the latter, and it is difficult to interpret these breeding peaks in terms of food supply.	Nectarinia venusta Variable Sunbird M-P&G 1251 Category (9) 164 records. Region A. X, I I Region B. II, 5; III, 2; IV, 1; VI, 1; X, 1; XII, 2 I2 Region C. I, 5; II, 4; III, 5; IV, 9; V, 6;		
	Nectarinia cyanolaema Blue-throated Brown Sunbird M-P&G 1268 Category (5) 6 records. Region B. IV, 2; VIII, 3; IX, 1 6 The few records for this forest species lie within the	VI, 2; VIII, 1; XI, 1		

Region E. V, 2

The few records for this forest species lie within the

peak periods for breeding in the previous species.

Region C records are mainly (29/33) January-May, in and after the rains, peaking in April. This is unexpected when 31/33 records are from Tabora and Iringa in central and southern Tanzania, and the pattern for Nectariniidae in other parts of this southern tropics climatic zone is pre-rains and early rains breeding September-November, peaking in October (Benson 1963). Region B records are mainly in the dry season, with 9/12 records December-March. The large number of Region D records are spread over all months, the fewest in September-October. Breeding is mainly in the rains in the vicinity of Nairobi, where 36/68 records are in the long rains April-July and 22/68 are in the short rains November-December. Excluding 24 records from the biassed Karen study, the same May peak emerges, but 22/44 records are November-December, suggesting that the short rains may be more important for breeding than the long rains. Arusha records peak in January (11/37), February (7/37) and July (8/37), but there is a bias here resulting from Beesley's exceptional activity prior to his April 1972 departure, in that all but three of his records are between 8 July 1971 and 4 April 1972, so that the comparative lack of records April-June may not be entirely real.

Nectarinia stuhlmanm Stuhlmann's Double-collared Sunbird M-P&G 1252 Category (4) 3 records.

Nectarinia mediocris Eastern Double-collared Sunbird M-P&G 1254 Category (7) 28 records.

Most Region D breeding is in and before the short rains, and all long rains (May-June) records are from below 2000 m.

Nectarinia preussi Northern Double-collared Sunbird M-P&G 1256 Category (5) 7 records.

Few records, but indicative of dry season breeding in this highland forest species.

Nectarinia chloropygia Olive-bellied Sunbird M-P&G 1257 Category (6) 20 records.

Region B. II, 1; IV, 2; V, 2; VI, 3; VII, 3; VIII, 2; IX, 2; X, 3; XI, 2 20

Ill-defined breeding seasons, with records spread fairly uniformly through February-November.

Nectarinia minulla Tiny Sunbird M-P&G 1258 Category (4) 2 records.

Region B. VII, 1; VIII, 1 2

Nectarinia loveridgei Loveridge's Sunbird M-P&G 1260 Category (3).

Region D. building 12. VIII.

Mackworth-Praed & Grant (1960) give September-February.

Nectarinia shelleyi Shelley's Double-collared Sunbird M-P&G 1246 Category (4) 1 record.

Nectarinia bifasciata Little Purple-banded Sunbird M-P&G 1241 Category (7) 27 records.

Ill-defined breeding seasons.

Nectarinia mariquensis Mariqua Sunbird M-P&G 1245 Category (7) 24 records.

Nectarinia pembae Violet-breasted Sunbird M-P&G 1243, 1244 Category (3).

Mackworth-Praed & Grant (1960) give Region D/E records as 'chiefly May, June, July, but any month May-January'.

Nectarinia habessinica Shining Sunbird M-P&G 1240 Category (4) 1 record.

Region D. XII, I I

Nectarinia cuprea Copper Sunbird M-P&G 1238 Category (7) 41 records.

Mainly rains breeding in Region B, with 34/39 records in the long rains in March-July.

Nectarinia tacazze Tacazze Sunbird M-P&G 1229 Category (7) 39 records.

No clear-cut breeding seasons emerge from these records, all of which are from above 2100 m. Region A breeding peaks after the rains, with 9/23 records November-December, though records are spread over all months except January and September, including a secondary peak in April at the beginning of the rains. Sessions (in litt.)

noted that this long-tailed species is present throughout the year at Mau Narok where there appears to be no non-breeding dress in males and two breeding peaks. 20/23 Region A records are his, mainly from his garden where he reported a high density of about twenty pairs breeding in 0.2 ha. Belcher (1939) reported the breeding of this and other sunbirds (N. mediocris, N. famosa, N. reichenowi) at South Kinangop from mid-May to the end of the year, peaking November-December and June, though he considered the latter peak far less important. 8/16 Region D records are his and the overall pattern for this region is similar to thatat Kinangop, though these still inadequate records indicatea more prolonged modal period November-January.

Nectarinia veroxii Mouse-coloured Sunbird M-P&G 1265 Category (6) 14 records.

Mainly in the rains, peaking in the wettest month. All ten sites described are inside houses or hanging from the roof of a verandah or garage. Though reported from elsewhere in other sunbird species, this habit is most prevalent at the Kenya coast, where it is the norm for this species, regular in *N. olivacea* and occasional in *Anthreptes collaris*. It is likely that the shelter provided by these nest-sites allows successful breeding in the wettest months, when rainfall is characteristically prolonged through much of the day, allowing little opportunity for the drying out of a waterlogged nest (for a fuller discussion see Britton & Britton 1977).

Nectarinia erythroceria Red-chested Sunbird M-P&G 1232 Category (8) 81 records.

Mainly breeding in the long rains in Region B, with 57/80 records March-July, peaking in April. There are records for all months, indicative of a secondary peak November-December, in and after the short rains, and pre-rains breeding in February.

Nectarinia pulchella Beautiful Sunbird M-P&G 1233 Category (8) 84 records.

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Region A. II, 2; III, 2; IV, 5; V, 5; VI, 2; VII, 2; IX, 3; X, 2; XI, 2; XII, 1 . . . 26
Region B. I, 2; II, 1; III, 2; V, 3; VI, 1; VII, 1; VIII, 4; IX, 3; XII, 1 . . . 18
Region C. I, 4; II, 2; III, 1; XI, 1; XII, 3 . II
Region D. I, 1; II, 1; III, 6; IV, 4; V, 12; VI, 1; VII, 1; VIII, 2; XI, 1 . . . 29
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Records are spread through much of the year in Regions A, B and D, but they peak in the early rains in Regions A (April-May) and D (March-May, especially May). Seasons are ill-defined in Region B, but there is no short rains breeding, and the virtual absence of short rains breeding in

Region D is noteworthy. 9/11 Region C records are in the rains December-February, and all records are November-March.

Nectarinia nectarinoides Smaller Black-bellied Sunbird M-P&G 1234 Category (4) 5 records.

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Region D. V, 1; VI, 1; VII, 1; VIII, 2 . 5
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Nectarinia famosa Malachite Sunbird M-P&G 1227 Category (7) 28 records.

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Region A. XI, 2; XII, 2 . . . . . . . . 4
Region D. V, 2; VI, 1; VII, 3; VIII, 4;
IX, 3; X, 9; XI, 1; XII, 1 . . . . . . 24
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All records are from above 2000 m. 19/24 Region D records are July-October, after the long rains, peaking in October before the short rains. All four Region A records are from above 2700 m November-December, after the rains. Two are from Mau Narok, where it is a seasonal visitor, arriving from the low country September-October (Sessions in litt.).

Nectarinia johnstoni Scarlet-tufted Malachite Sunbird M-P&G 1228 Category (7) 21 records.

Coe (1961) noted that this high altitude species breeds in fine weather on Mt Kenya July-August and December-February. We can add little to this as there are no cards for this species. Records from all Region D localities show that the long rains are avoided, and that breeding is confined to the dry months of July-October and January-February, and the end of the short rains in December. Both Region B records are December-January after the short rains.

Nectarinia superba Superb Sunbird M-P&G 1237 Category (5) 8 records.

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Region B. III, 1; IV, 2; V, 1; VII, 1; VIII, 1; IX, 2 . . . . . . . . . . . . . . . 8 Few records, but seasons are not well-defined.
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Nectarinia kilimensis Bronze Sunbird M-P&G 1230 Category (8) 90 records.

Mainly breeding early in the long rains and in the short rains in Region B, with 8/22 records March-April and 8/22 October-November. Region D records are spread over all months, peaking in the long rains March-June (37/60). Records from the vicinity of Nairobi are similarly spread over all months, peaking in March (5), April (11),

June (6), July (4) and December (4). Only six are from the biassed Karen study, none of them in April, so that the overall April peak in Region D is apparently real. It is noteworthy that all four December records for this region are from Nairobi, and that there is no short rains breeding reported from Arusha, where peaks are in April (3/8 records) and October (2/8). The flowering of Erythrina abyssinica and other trees, shrubs and herbs probably accounts for the April peak in this mainly nectarivorous species.

Nectarinia reichenowi Golden-winged Sunbird M-P&G 1235 Category (7) 26 records.

A highland species with regular movements to lower levels in the cool wet months of the long rains. Region A records are August-March, avoiding the wettest, coolest months, and peaking November-December. The five Region D records in the long rains in April and June are from below 2000 m. The few records from higher altitudes in Region D indicate that the rains are avoided, with 4/6 in January.

Zosteropidae White-eyes

Zosterops senegalensis Green White-eye M-P&G 1219, 1220, 1221 Category (7) 48 records.

Region B records are spread over all months except August and October with 29/34 January-July, in the driest and wettest months. Two of the Region D records refer to the race *vaughani*, endemic to the island of Pemba. Pakenham (1943) found *vaughani* breeding in all months between August and April, and Mackworth-Praed & Grant (1960) describe the season as indefinite, mostly October-December, but also March-July. The extent to which either of these generalizations refers to eggs and young is uncertain, but together they indicate an ill-defined season with records in all months.

Zosterops poliogastra Montane White-eye M-P&G 1222, 1223, 1224, 1225 Category (7) 48 records.

Region D. I, 4; III, 5; IV, 9; V, 14; VI, 9; VII, 1; VIII, 1; IX, 1; X, 2; XI, 1; XII, 1 48

Breeding is mainly in the long rains, with 37/48 records March-June, peaking in May. 28/35 records from the vicinity of Nairobi are March-June, with a peak in May (12). The twelve biassed Karen records also peak in May (5), and if unbiassed Nairobi records are analysed alone, 17/23

are March-June. There is virtually no short rains breeding, and all four January records are from above 2400 m, where the months of heaviest rainfall are probably avoided.

Zosterops abyssinica Yellow White-eye M-P&G 1219 Category (7) 21 records.

Region D. II, 1; III, 2; IV, 6; V, 9; VI, 3 . 21
Breeding mainly in the long rains with 20/21 records
March-June, peaking in May; but 14/21 records are
from the biassed Karen study.

As arboreal insect-eaters, Zosterops spp. might be expected to breed mainly in the rains. Most Region D breeding of poliogastra and abyssinica is in the long rains, and there is hardly any short rains breeding. Seasons are ill-defined elsewhere, including Region D breeding of vaughani on atypical Pemba.

Ploceidae, Ploceinae

Amblyospiza albifrons

Category (9) 133 records.

Weavers, Bishops, Widows

Grosbeak Weaver M-P&G 1358

Seasons are prolonged and rather ill-defined, though they peak March-June and December in Region D, and April-June in Region B. Breeding in Region E is also in the rains, but peaking late, which is a pattern exhibited by other ploceids in this region (see below). Aquatic plants are likely to provide both nesting sites and seeds throughout the year for this riparian breeder.

Ploceus baglafecht Baglafecht Weaver M-P&G 1323, 1347, 1348, 1349 Category (9) 135 records.

Virtually all Region A, B and C records are in the rains, peaking early in the rains in April (7/15) in Region A. Region D records fall in all months except August, but mainly February–June (67/111) with a peak in May. There is no short rains peak. Unbiassed records from the vicinity of Nairobi also peak in May (17/53), but there are records for all months except August.

Ploceus bertrandi Bertram's Weaver M-P&G 1352 Category (3).

Region C. Lynes (1934) gives two females 'soon to breed' in XI and XII.

Ploceus luteolus Little Weaver M-P&G 1324 Category (6) 14 records. Region A. V, 2; VI, 1; VIII, 2; XI, 1	Ploceus castanops Northern Brown-throated Weaver M-P&G 1330 Category (7) 43 records. Region B. II, 5; III, 5; IV, 12; V, 12; VI, 3; VII, 1; VIII, 1; X, 1; XI, 1; XII, 2 . 43 Records for this swamp species are for all months except January and September, but mainly in the long rains February-June, peaking April-May (24/43 records).
Category (7) 25 records. Region B. II, 5; III, 4; IV, 4; V, 2; VI, 1; VII, 8; VIII, 1	Ploceus taeniopterus Northern Masked Weaver M-P&G 1316 Category (4) 2 records. Region A. I, 1; V, 1
Ploceus subaureus Golden Weaver M-P&G 1341 Category (7) 41 records. Region D. I, 1; II, 1; III, 9; V, 1; VII, 2; VIII, 1; X, 4; XI, 4; XII, 1 24 Region E. V, 8; VIII, 6; XI, 3 17 Ill-defined breeding seasons.	Region B. III, 17; IV, 15; V, 2; VI, 2 . 36 Region C. IV, 4 4 Region D. I, 5; II, 3; III, 14; IV, 120; V, 7; VI, 16; VII, 12; XII, 1 178 Mainly breeding in the long rains, March-June in Region B and March-July in Region D.
Ploceus xanthops Holub's Golden Weaver M-P&G 1342 Category (8) 67 records. Region A. IV, 2; V, I 3 Region B. II, I; IV, 2; V, 2; VI, I; X, I 7 Region D. I, 5; II, 4; III, 12; IV, 15; V, 7; VIII, I; X, 4; XI, I; XII, 8 57 Rains breeding in Regions A and B, and peaking in the long rains in Region D, where 34/57 records are March-May. Unbiassed records from the vicinity of Nairobi peak March-April (21/38).	Ploceus velatus Vitelline Masked Weaver M-P&G 1321, 1322 Category (9) 119 records. Region A. VI, 2; VIII, 1
Ploceus aurantius Orange Weaver M-P&G 1334 Category (7) 35 records. Region B. I, 1; II, 1; III, 13; IV, 15; V, 4; XI, 1	Ploceus heuglini Heuglin's Masked Weaver M-P&G 1318 Category (4) 3 records. Region A. V, 1; VI, 2

March-May.

Ploceus bojeri Golden Palm Weaver M-P&G 1331 Category (9) 207 records.

> Region D. I, 40; IV, 15; X, 62; XI, 15 . 132 Region E. I, 1; IV, 12; V, 16; VI, 4; VII, 9; VIII, 22; IX, 2; X, 7; XI, 2 . .

A prolonged season in Region E, but mainly in the rains, with a late rains peak in August, as is the case with several other ploceids.

Ploceus castaneiceps Taveta Golden Weaver M-P&G 1333 Category (9) 174 records.

Region D. I, 1; II, 5; III, 3; IV, 3; V, 2; X, 150; XI, 7; XII, 3 . . . 174 Breeding in and before both rains.

Ploceus spekei Speke's Weaver M-P&G 1314 Category (9) 106 records.

Region B. V, 1; VI, 5 . . . Region D. II, 1; III, 28; IV, 30; V, 12; VI, 6 VII, 5; X, 3; XI, 6; XII, 9 . . . 100

Region D records are February-July and October-December, with a long rains peak March-May (70/100) and a short rains peak November-December (15/100). The few Region B records are in the long rains, and short rains breeding in Region D is not proportionate to the rainfall.

Ploceus spekeoides Fox's Weaver M-P&G Category (3).

Region A. building VI.

Mackworth-Praed & Grant (1960) give breeding activity June-August.

Ploceus cucullatus Black-headed Weaver M-P&G Region B. II, 1; IV, 6; V, 6; VI, 3; VIII, 2; IX, 2; X, I 21 1312, 1313 Category (10) 851 records. Region A. IV, 2; VIII, 100 15/21 records are in the long rains April-June, with a . 102 Region B. II, 3; III, 4; IV, 8; V, 6; VI, 14; secondary peak August-September before the short rains. VII, 1; VIII, 1; IX, 1; X, 4; XI, 1; XII 1 44 Region C. II, 2; III, 1; V, 1; X, 1; XII, 1 . Ploceus bicolor Dark-backed Weaver M-P&G 1335 Region D. II, 1; III, 14; IV, 269; V, 103; Category (4) 2 records. VI, 2; VII, 2; VIII, 1; IX, 2; X, 3; XI, 62 459 Region D. VIII, I I Region E. VII, 240 240 Region E. IV, 1 . . . Region B and D records fall in most months but mainly It is worth noting five records of nest building in Region in the rains, peaking February-June and October in B in March (3), April and June. Breeding is mainly in the Region B and March-May and October-November in rains. Region D. Ploceus tricolor Yellow-mantled Weaver M-P&G 1353 Vieillot's Black Weaver M-P&G Ploceus nigerrimus Category (4) 2 records. 1344 Category (7) 39 records. Region B. V, r; VI, r . . . Region B. I, 1; II, 8 III, 3; IV, 7; V, 3; Both records are in the long rains. VI, 1; VII, 3; IX, 9; X, 3; XII, 1 . . . 39 A forest-edge weaver with rather ill-defined breeding seasons, but peaking in and before the rains February-July Ploceus ocularis Spectacled Weaver M-P&G 1377 and September-October. Category (8) 84 records. Region A. VI, r . Ploceus wevnsi Weyns' Weaver M-P&G 1345 Category Region B. II, 2; III, 7; IV, 13; V, 8; VI, 5; VII, 3; VIII, 1; XI, 1; XII, 1 . . 41 Region D. I, 2; II, 1; III, 2; IV, 8; V, 9; Region B. Mackworth-Praed & Grant (1960) mention breeding condition in VII. VI, 7; VII, 1; IX, 2; X, 3; XI, 1; XII, 1 37 Region E. VIII, 3; IX, 1; X, 1 Ploceus melanocephalus Yellow-backed Weaver M-P&G Breeding is mainly in the long rains in Region B, with 1325 Category (9) 144 records. 33/41 rccords March-June, peaking in April. Records in Region B. I, 1; II, 3; III, 5; IV, 19; V, 82; Region D are spread over all months, peaking April-June VI, 17; VII, 12; VIII, 1; IX, 2; X, 1; (24/38), but all 13 of the biassed Karen records are April-XII, 1 144 June, accounting for much of this peak; a Region E peak Mainly in the long rains March-July, peaking April-June in August, late in the rains, as with other ploceids. (118/144 records). Ploceus nigricollis Black-necked Weaver M-P&G 1336 Golden-backed Weaver M-P&G 1326 Ploceus jacksoni Category (8) 71 records. Category (9) 394 records. Region B. II, 1; III, 3; IV, 16; V, 11; VI, 6; Region A. VIII, 1 . VII, 3; VIII, 1; XII, 1 . . . 42 Region B. I, 1; II, 13; III, 2; IV, 116; V, 104; Region D. I, 1; II, 1; III, 6; IV, 10; V, 5; 25 IX, 2 Region C. II, 1; III, 4; IV, 3; IX, 1; XII, 1 10 Region E. V, 1; VII, 1; VIII, 2 Region D. III, 26; IV, 1; V, 100; VI, 11 . 138 Breeding is mainly in the long rains, March-July in Breeding in the long rains in Region D in March-June; Region B, peaking April-May (27/42), and March-May mainly in the late rains in Region C in March-April; and (21/25) in Region D, peaking in April. mainly in the rains in Region B, February-June and November, with a pronounced peak April-May in the long Black-billed Weaver M-P&G Ploceus melanogaster rains. 1346 Category (5) 10 records. Region A. V, 1; VI, 1; VII, 1; IX, 1; X, 2; Ploceus rubiginosus Chestnut Weaver M-P&G 1327 XII, 1 7 Category (10) 1368 records. Region B. I, 2; VI, I Region A. V, 20; VI, 20; VII, 1 There are few records for this forest weaver, but they are indicative of a prolonged breeding season in Region Region D. IV, 40; V, 1195; VI, 49; VII, 40 1324 A in and after the rains. Rains breeding in Region A, long rains breeding in Region D, and late rains breeding in Region C. Strange Weaver M-P&G 1339 Category Ploceus alienus Compact Weaver M-P&G 1350 (4) 2 records. Ploceus superciliosus

Category (7) 21 records.

Region B. I, 1; II, 1

These Rwenzori records from an altitude of 1900–2000 m are indicative of dry season breeding.

Ploceus insignis Brown-capped Weaver M-P&G 1351 Category (6) 16 records.

There are too few records for this insectivorous forest weaver, but they are indicative of ill-defined seasons.

Typically, *Ploceus* weavers breed in the rains, mainly the long rains, but forest species tend to have less defined breeding seasons.

Malimbus nitens Blue-billed Malimbe M-P&G 1357 Category (3).

Region B. Mackworth-Praed & Grant (1960) give III onwards.

Malimbus rubricollis Red-headed Malimbe M-P&G 1356 Category (4) 5 records.

Region B. IV, 1; V, 2; VIII, 2 . . . 5

Malimbus malimbicus Crested Malimbe M-P&G 1355 Category (4) 4 records.

Region B. I, 1; IV, 1; V, 2 . . . 4

The few records for these three insectivorous forest malimbes are indicative of breeding in and after the long rains.

Anaplectes rubriceps Red-headed Weaver M-P&G 1359 Category (6) 20 records.

These few records for this mainly insectivorous, drycountry species are indicative of breeding in and around the rains.

Quelea cardinalis Cardinal Quelea M-P&G 1362 Category (9) 157 records.

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      Region A. III, 1; VI, 3
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Rains breeding throughout, with only a single long rains season in both Region B and D. Its nest site in long grass or rank herbage, and its diet of grass seeds and other small grains, act to restrict its breeding seasons to wet periods when grasses grow rapidly and flower. Similar ecology accounts for similar breeding seasons in Q. quelea and various Euplectes species, though some Euplectes have

a more catholic diet of seeds and insects, especially when feeding young. Pre-nuptial moult of elaborate plumage provides an added constraint on the breeding seasons of *Euplectes* spp.

Quelea quelea Red-billed Quelea M-P&G 1360 Category (10) millions.

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Region C. I, 1; III, *; IV, *.
Region D. I, *; IV, *; V, *; VI, 4.
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* huge numbers, in tens of thousands or hundreds of thousands.

Breeding in the late rains in Reigon C and in both reins in Region D. Breeding is stimulated by the appearance of green grass (Marshall & Disney 1957).

Euplectes afer Yellow-crowned Bishop M-P&G 1369 Category (6) 18 records.

Less confined to the rains than most *Euplectes*, but in the the late rains in Regions A and C and mainly in the long rains May-June in Region D.

Euplectes albonotatus White-winged Widowbird M-P&G 1373 Category (8) 59 records.

Rains breeding in Region C, and mainly in the long rains March-June in Region D, peaking in May; evidence of short rains and between-rains breeding on a smaller scale.

Euplectes ardens Red-naped Widowbird M-P&G 1375 Category (9) 139 records.

Rains breeding in Regions B and C, and mainly in the long rains April-June in Region D, peaking in May. A secondary peak in January follows the short rains.

Euplectes axillaris Fan-tailed Widowbird M-P&G 1370 Category (8) 59 records.

Rains breeding throughout including short rains breeding in Region B.

May-October, peaking in August. Seasons are not wellgory (8) 53 records. Region A. V, 1; VII, 2; VIII, 1; X, 1 defined in Region D, though the only months with more . 5 Region D. I, 1; II, 1; III, 7; IV, 17; V, 12; than a single colony are in the rains May-June and Nov-VI, 7; VII, 1; XI, 1; XII, 1 . . . 48 ember. The late rains breeding peak for ploceids in Region Rains breeding throughout, peaking in the long rains E is especially clear in this species for which data collected March-June in Region D, with trivial breeding activity by resident Mombasa ornithologists are available for in and after the short rains. several years. Eupletes diadematus Fire-fronted Bishop M-P&G 1368 Euplectes orix Southern Red Bishop M-P&G 1363 Category (5) 8 records. Category (8) 53 records. Region D. V, 4; VI, 1; XII, 3 Region B. IV, 1; V, 5; VI, 4 . . . Region C. II, 7; III, 2; V, 4 13
Region D. V, 8; VI, 22 30 Breeding in both rains. Euplectes gierowii Black Bishop M-P&G 1366 Category Rains breeding throughout with evidence of breeding in (5) 7 records. the short rains. Region B. IV, 1; VII, 1; VIII, 1; X, 1; XII, 1 5 Euplectes fransiscanus Northern Red Bishop M-P&G Region C. VI, I I 1363 Category (4) 3 records. Region D. V, I . Region B. IV, 1; V, 1; IX, 1 . Euplectes hartlaubi Marsh Widowbird M-P&G 1374 Euplectes progne Long-tailed Widowbird M-P&G Category (5) 6 records. 1377 Category (4) 5 records. Region B. IV, I; V, I; VII, I . 3 Region D. IV, 2; V, 3 . . . These few records are in the long rains. The few records available for this and the previous species do not conform to the overall Euplectes pattern of Euplectes jacksoni Jackson's Widowbird M-P&G 1378 rains breeding, though 8/13 records are in wet months. Category (6) 19 records. Region A. I, 1; VIII, 2; IX, 3; XI, 1 . 7 Euplectes hordeaceus Black-winged Red Bishop M-P&G Region D. I, 1; IV, 4; V, 6; VI, 1 . . . 12 1365 Category (7) 47 records. Mainly in the rains. All Region A records are late in the Region A. VII, 1; VIII, 1 rains or in the subsequent dry season. Region B. IV, 1; V, 2; VI, 3 . . . 6 Region C. II, 1; III, 3; IV, 4; V, 8; VI, 1 . 17 Euplectes and Quelea species have a clear long rains or Region D. I, 4; III, 1; IV, 4; V, 2; VI, 2; rains breeding season (discussed under Q. cardinalis). VII, 1; XII, 1 Region E. IV, 1; V, 2; VI, 1; VII, 1; Anomalospiza imberbis Parasitic Weaver M-P&G 1405 VIII, 1; IX, 1 Category (5) 10 records. Rains breeding throughout, though late rains and Region B. II, 1; V, 2; VI, 1 immediately following the rains in Region C, and with a Region D. I, 3; V, 1; VI, 1; X, 1 . . . 6 breeding season in and after the short rains in Region D Breeding seasons of this species are likely to reflect those additional to a more prolonged long rains season. of the host species, which are usually rains breeding grassland warblers. Euplectes macrourus Yellow-mantled Widowbird M-P&G 1372 Category (5) 7 records. Ploceidae, Bubalornithinae **Buffalo Weavers** Region B. VI, 2; VII, 3; VIII, 1 . 6 Bubalornis niger Red-billed Buffalo Weaver M-P&G Region C. VI, I 1285 Category (6) 11 records. These few records are indicative of a breeding season 1 beginning late in the rains and continuing into the subsequent dry months. Region D. III, 1; IV, 1; V, 5; XII, 1 Rains breeding throughout. Euplectes nigroventris Zanzibar Red Bishop M-P&G 1364 Category (8) 75 records. Bubalornis albirostris White-billed Buffalo Weaver Region D. I, 1; II, 2; III, 2; IV, 1; V, 2; M-P&G 1284 Category (4) 2 records. Region A. IX, 1 . . . Region E. V, 5; VI, 3; VII, 3; VIII, 36; Region D. VII, I

Rains breeding in Region E, with a prolonged season

Euplectes capensis

Yellow Bishop M-P&G 1367 Cate-

Dinemellia dinemelli White-headed Buffalo Weaver M-P&G 1286 Category (7) 39 records. Region A. V, I I Region C. XII, 2	Dry-country ploceids of the genera Bubalornis, Dinemellia, Plocepasser, Histurgops and Pseudonigrita clearly favour the rains (especially the long rains) for breeding. Passer domesticus House Sparrow M-P&G 1293 Category (3). Region D. Mackworth-Praed & Grant (1960) give breeding mostly in X-I; P. d. indicus is an introduced species on Zanzibar Island which has been discussed earlier (see Corvus splendens).
Ploceidae, Passerinae Sparrow Weavers, Social Weavers, Sparrows Plocepasser mahali White-browed Sparrow Weaver M-P&G 1287 Category (7) 41 records. Region A. IV, 1; VIII, 2 3 Region D. II, 1; III, 1; IV, 6; V, 11; VI, 14; VII, 3; IX, 1; XII, 1 38 Rains breeding in Region A, and virtually confined to the long rains in Region D (31/38 records April-June). Plocepasser superciliosus Chestnut-crowned Sparrow	Passer motitensis Rufous Sparrow M-P&G 1294, 1295 Category (7) 49 records. Region A. IV, I
Weaver M-P&G 1288 Category (4) 4 records. Region A. III, 1; IV, 1; VIII, 1; IX, 1 . 4 These few records are in the rains. Plocepasser donaldsoni Donaldson-Smith's Sparrow Weaver M-P&G 1289 Category (5) 6 records. Region D. I, 1; VI, 1; VII, 1; XI, 1; XII, 2 6 These few records are indicative of breeding in both rains.	Passer griseus Grey-headed Sparrow M-P&G 1300-1303 Category (8) 83 records. Region A. I, 2; II, 1; III, 1; IV, 1; V, 1; X, 1; XI, 1; XII, 3
Histurgops ruficauda Rufous-tailed Weaver M-P&G 1290 Category (8) 82 records. Region C. I, 13; II, 4; VI, 1; VIII, 5; X, 1; XI, 1; XII, 2	Region D. I, 3; III, 2; IV, 2; V, 6; VI, 5; VII, 2; X, 1; XI, 2; XII, 3 26 Breeding in Region B is mainly in the long rains, with 28/33 records April-June, and all records April-August, peaking in May. Region D records are in and around the rains March-July and September-January, peaking May-June (11/26) and December-January (6/26). Most Region A records are in the dry season, and Region C records are equally divided between wet and dry periods.
Pseudonigrita arnaudi Grey-headed Social Weaver M-P&G 1291 Category (9) 143 records. Region A. VIII, 1; XII, 10	These contradictions may result from its loose association with human dwellings in some areas and its catholic diet. Modified peri-urban and farmland habitats are likely to be more perennially verdant than natural habitats, with less marked seasonal variations in food supply. Passer eminibey Chestnut Sparrow M-P&G 1306 Category (9) 179 records.
breeding in Region D in February, and post-rains breeding in Region C April-May. Pseudonigrita cabanisi Black-capped Social Weaver M-P&G 1292 Category (5) 8 records. Region D. I, I; III, I; IV, I; V, I; VIII, I; XI, I; XII, 2 8 Few records spread over seven months, but indicative of	Region A. I, 5; V, 5; VI, 5

for by its habit of utilising abandoned ploceid nests rather than building its own, though the peak is earlier than

breeding in both rains.

Few records spread over seven months, but indicative of

Amadina fasciata and Lonchura malabarica which have Hypochera chalybeata Red-billed Firefinch Indigobird a similar habit (see below). All Region B records are late M-P&G 1435, 1436 Category (6) 14 records. in the long rains in June, but the few records from Regions Region B. V, 2; VI, 2; VII, 2 . . . A and C are inconclusive. Region D. IV, 1; V, 3; VI, 3; VII, 1 All records are during and after the long rains. Petronia pyrgita Yellow-spotted Petronia M-P&G Hypochera funerea African Firefinch Indigobird 1308 Category (5) 9 records. M-P&G 1434, 1438 Category (4) 1 record. Region C. VI, 1; XI, 1 . Region C. III, I Region D. III, 1; IV, 2; V, 1; XI, 3 . These few records clearly indicate breeding in both Hypochera purpurascens Jameson's Firefinch Indigobird rains in Region D. M-P&G 1438 Category (4) 3 records. Region A. VI, 3 . . Petronia superciliaris Yellow-throated Petronia M-P&G The breeding of all viduines is virtually confined to the 1307 Category (4) 2 records. rains (long rains in Regions B and D). The elaborate Region D. X, 1; XII, 1 breeding dress of whydahs is assumed before the rains, Sparrows and petronias have a mixed diet of insects which are not themselves the proximate factor initiating and seeds. Breeding is typically in the rains, especially the this moult. The growth of the tail is likely to take sufficiently long rains. long that a moult initiated at the onset of rains would be incomplete by the time that their estrildid hosts are breeding. This pre-nuptial moult is likely to act as a Speckle-fronted Weaver M-P&G Sporopipes frontalis constraint on the breeding seasons of these species (and to 1311 Category (6) 15 records. a lesser extent indigobirds) so that these seasons are likely Region C. I, 1; II, 1; V, 1; VI, 1; VII, 2; to be still less variable than those of their hosts. VIII, 1; XII, 1 8 Region D. III, 2; IV, 1; V, 1; VI, 1; VII, 1; Estrildidae Waxbills and allies The inadequate records indicate that this dry-country Clytospiza monteiri Brown Twinspot M-P&G 1389 species may breed at any time of the year in Region C, Category (3). whether it is wet or dry, but that it may breed mainly in Region B. Mackworth-Praed & Grant (1960) give the rains in Region D. VI-X. Hypargos niveoguttatus Peters' Twinspot M-P&G 1406 Ploceidae, Viduinae Whydahs, Indigobirds Category (4) 3 records. Pin-tailed Whydah M-P&G 1441 Vidua macroura Region E. V, 2; VII, 1 Category (6) 18 records. Region B. IV 1; X, 1; XI, 1 . . . 3 Mandingoa nitidula Green Twinspot M-P&G 1407 Region C. I, 2; III, 1; XII, 1 . Category (4) 2 records. Region D. IV, 5; V, 3; VI, 1; VII, 2 . Region D. VI, 1 All records are in the rains. Region E. VII, I The few records for this and the previous species are Vidua fischeri Straw-tailed Whydah M-P&G 1443 Category in the rains. (5) 7 records. Cryptospiza salvadorii Abyssinian Crimson-wing Region D. IV, 2; V, 2; VI, 3 . M-P&G 1399 Category (5) 8 records. All records are in the long rains. Region A. X, 1; XI, 1; XII, 1 . Region D. I, 1; II, 1; VIII, 1; IX, 2 . 5 Steel-blue Whydah M-P&G 1442 Vidua hypocherina All breeding records of this high altitude forest-edge Category (5) 7 records. species are in dry months following the rains. Region A Region A. VI, 1; IX, 1 . . . 2 records are from 2500 m or above but some Region D Region B. VI, 1; VII, 1 . . . 2 records are from as low as 2000 m. Region D. V, 1; VI, 2 . . . Rains breeding in Region A and long rains breeding in Cryptospiza reichenovii Red-faced Crimson-wing Regions B and D. M-P&G 1398 Category (4) 2 records. Region B. III, 2 Vidua paradisaea Long-tailed Paradise Whydah

5

M-P&G 1444 Category (4) 5 records.

Region D. VI, 5 . . .

All records are at the end of the long rains.

Cryptospiza jacksoni Dusky Crimson-wing M-P&G

1400 Category (4) 1 record.

Region B. V, 1

Pyrenestes ostrinus Black-bellied Seed-cracker M-P&G Breeding in both rains in Region D and in the long rains 1393-1395 Category (5) 7 records. in Region B. Most Region C breeding is in the rains or Region B. III, 2; IV, 2; V, 1; IX, 2. immediately after, with 12/15 records January-June. The few records for this and the previous two species are Pytilia afra indicative of breeding early in the rains. Orange-winged Pytilia M-P&G 1409 Category (5) 10 records. Region C. VI, 1; VIII, 1 Nigrita canicapilla Grey-headed Negro-finch M-P&G Region D. III, 2; IV, 2; V, 1; VI, 1; 1386 Category (6) 16 records. VII, 1; X, 1 Region A. III, 1; IV, 1; V, 1; VI, 3; VII, 1 Both Region C records are in the dry season, but 6/8 Region B. IV, 1; V, 2; VI, 1; X, 3 . . . Region D records are in the long rains March-June. Region D. VIII, 1; X, 1 . Rains breeding in Regions A and B, but dry season Estrilda melanotis Yellow-bellied Waxbill M-P&G breeding in Region D. The latter are from Arusha, and 1417 Category (6) 17 records. there are two additional records of nest building at Arusha Region B. IV, 1; VII, 1; VIII, 1 and Kilimanjaro in early and mid September. The Kilima-Region D. I, 1; V, 3; VI, 7; VII, 2; XII, 1 . 14 njaro record is from 2800 m but Arusha records are from All Region D records are for the latter part of the rains as low as 1600-2000 m. All but one of the Region A and B or immediately after, in May-July and December-January. records are from below 1800 m. Estrilda paludicola Fawn-breasted Waxbill M-P&G White-breasted Negro-finch M-P&G Nigrita fusconota 1422 Category (5) 7 records. 1388 Category (4) 3 records. Region A. XI, 1 . Region B. IV, 1; VII, 1; VIII, 1 Region B. I, 1; II, 1; III, 1; V, 1; X, 1; XI, 1 Red-headed Bluebill M-P&G Spermophaga ruficapilla Estrilda nonnula Black-crowned Waxbill M-P&G 1425 1391 Category (5) 8 records. Category (6) 14 records. Region B. I, 1; IV, 1; VI, 1; VII, 1; IX, 1; Region B. I, 1; III, 2; IV, 3; V, 3; VII, 1; X, 2 . . Seasons are rather ill-defined, but all months with more Most Region B breeding is in the rains April-July and than a single record are in the rains March-May (8/14) September-October. and October. Grey-headed Olive-back M-P&G Nesocharis capistrata Estrilda atricapilla Black-headed Waxbill M-P&G 1428 Category (4) 1 record. 1424 Category (4) 2 records. Region A. VI, 1 Region D. I, 1; XI, 1 Estrilda rhodopyga Crimson-rumped Waxbill M-P&G Nesocharis ansorgei White-collared Olive-back M-P&G 1420 Category (5) 10 records. 1429 Category (3). Region B. V, I; VII, I Region B. building, three-quarters complete, Region C. I, 1; III, 1; IV, 1; V, 2 . 12.IX. Region D. III, 1; IV, 1; VIII, 1 . Amadina fasciata Cut-throat M-P&G 1402 Category These few records are indicative of breeding in or (7) 43 records. immediately after the long rains. Region D. III, 1; IV, 2; V, 3; VI, 8; VII, 23; Black-rumped Waxbill M-P&G Estrilda troglodytes VIII, 5; XII, 1 43 1419 Category (4) 1 record. Rains breeding with a pronounced peak at the end of the long rains. This species' habit of laying in abandoned Region B. VI, 1 Mackworth-Praed & Grant (1960) give VIII-XI for ploceid nests probably accounts for the late breeding peak, Region A, and there is a second Region B record of nest at a time when recently vacated nests are readily available. Moreau (1950) noted this late breeding and considered it building in June. possible that this species is stimulated to breed by the sight Estrilda astrild Waxbill M-P&G 1418 Category (8) of a profusion of potential homes. 72 records. Region A. V, 2; VI, 1; VII, 1; IX, 1; XI, 1 . Green-winged Pytilia M-P&G 1410 Pytilia melba Region B. III, 1. IV, 2; V, 3; X, 2 . . . 8 Category (7) 31 records. Region C. III, 1 . . . Region A. III, 2; V, I . Region D. I, 1; II, 3; III, 4; IV, 10; V, 18; Region C. I, 3; II, 1; III, 4; IV, 2; V, 2; VI,

15

VI, 12; VII, 4; VIII, 1; XI, 3 . . . 56

Region E. V, I

1; VIII, 1; X, 1

Region D. I, 1; IV, 2; V, 5; VI, 4; XII, 1

Rains breeding throughout, involving both long and short rains in Regions B and D. An especially marked long rains peak in Region D, with 40/56 records April-June, peaking in May and including only three biassed April records from Karen.

Estrilda erythronotos Black-cheeked Waxbill M-P&G 1427 Category (6) 13 records.

All breeding is in the long rains in Regions B and D and in the rains in Region C.

Uraeginthus ianthinogaster Purple Grenadier M-P&G 1433 Category (7) 32 records.

All Region C records are in the rains December-April, 15/20 Region D records are in the long rains March-June, and all Region A records are in the pre-rains and early rains February-June.

Uraeginthus angolensis Cordon-bleu M-P&G 1430 Category (6) 15 records.

All Region D records are from eastern Tanzania in localities peripheral to Region C, so that all of these February-May records may well refer to the rains.

Uraeginthus bengalus Red-cheeked Cordon-bleu M-P&G 1431 Category (8) 92 records.

Mainly breeding in the rains including a marked short rains peak in Region B (5/14 records). All Region C records are January-May in the late rains and immediately after, with a pronounced peak in March (16/31). Some of the long rains peak in Region D March-July (24/30 records) is accounted for by nine biassed Karen records.

Uraeginthus cyanocephalus Blue-headed Cordon-bleu M-P&G 1432 Category (6) 12 records.

Breeding in the rains, except for two May records from Dodoma in Region C which are in the early dry season.

Lagonosticta rufopicta Bar-breasted Firefinch M-P&G 1414 Category (4) 2 records.

Region A. V, I I Region B. V, I; I

Both records are in the rains. Mackworth-Praed & Grant (1960) give records from Nile Province, Uganda, probably in Region A, June-October.

Lagonosticta senegala Red-billed Firefinch M-P&G 1413 Category (8) 75 records.

All Region C records are in the mid or late rains, and 17/19 Region B records are in March-July in the long rains. There are Region D records for all months, but peaking in the long rains in March-June (36/52), only nine of these being biassed Karen data. There is a barely discernible short rains peak in Region D.

Lagonosticta rhodopareia Jameson's Firefinch M-P&G 1411, 1412 Category (4) I record.

Region D. VI, I I

Lagonosticta rubricata African Firefinch M-P&G 1411 Category (7) 18 records.

Few records except in Region D where 13/16 are in the long rains March-July.

Amandava subflava Zebra Waxbill M–P&G 1421 Category (6) 20 records.

The only months with more than a single record are April-June in Region D, indicative of long rains breeding with a rather late peak in June, perhaps explained by its habit of sometimes utilizing abandoned nests of other species, especially ploceids.

Ortygospiza atricollis Quail Finch M-P&G 1403 Category (6) 18 records.

Mainly in the rains; in particular the Region D peak in the long rains April-May. Lonchura oryzivora Java Sparrow M-P&G 1385 Category (3).

Region D. Mackworth-Praed & Grant (1960) give V-VIII for this introduced species on Zanzibar Island. It is noteworthy that this long rains breeding season is quite different from those of other introduced species there, though typical of estrildids in East Africa (see *Corvus splendens*).

Lonchura malabarica Silverbill M-P&G 1383 Category (7) 51 records.

Region D. III, 1; IV, 3; V, 5; VI, 14; VII, 26 VIII, 2 51

Breeding in the long rains, with a late peak June-July. This lateness may be ascribed to its habit of nesting in abandoned ploceid nests (see *Amadina fasciata*).

Lonchura griseicapilla Grey-headed Silverbill M-P&G 1384 Category (4) 1 record.

Region D. V, I

Lonchura fringilloides Magpie Mannikin M-P&G 1382 Category (3).

Mackworth-Praed & Grant (1960) give Uganda records (Region A/B) April-September.

Lonchura bicolor Blue-billed Mannikin M-P&G 1380, 1381 Category (8) 66 records.

Breeding mainly in the rains, with records in both rains in Region B; in all months except February and September in Region D, peaking in the long rains March-June (37/50) and in the short rains December-January (6/50); mainly in May and July in Region E. More than half of the Region D records (22/41) are from the biassed Karen study, but a long rains peak March-June is still evident if these records are ignored.

Lonchura cucullata Bronze Mannikin M-P&G 1379 Category (9) 116 records.

There are records in all months in Region D and in all months except January in Region B. Seasons are less defined than in other estrildids, though there are long rains peaks April-June (34/54 Region B, 25/50 Region D).

Fringillidae Buntings, Canaries, Seed-eaters

Emberiza flaviventris Golden-breasted Bunting M-P&G
1469 Category (7) 45 records.

Rains breeding in Region C, where all records are October-April; a long rains peak in Region D, where 13/25 records are in April, only two of these April records being biassed. Insects are probably more important than seeds in the diet of this and other buntings.

Emberiza poliopleura Somali Golden-breasted Bunting M-P&G 1470 Category (4) 2 records.

Emberiza tahapisi Cinnamon-breasted Rock Bunting M-P&G 1476 Category (7) 22 records.

Breeding at the end of the rains and early in the dry season in Region C, contrasting with mainly rains breeding in Region D (for discussion see under *Eremopterix leucotis*).

Serinus mozambicus Yellow-fronted Canary M-P&G 1448 Category (8) 52 records.

Mainly in the long rains in Region B, with 13/21 records April–July, but secondary peaks in October (short rains) and January (dry). Region C records peak in the rains in February, but the main season is late in the rains, extending into the dry season February-June (20/22). The few records from other regions are mainly in the rains.

Serinus atrogularis Yellow-rumped Seed-eater M-P&G 1459 Category (7) 36 records.

Mainly in the long rains March-June in Regions B and D, with 6/7 and 18/22 records respectively, peaking late in the rains May-June. Mainly in the rains in Region C.

Serinus leucopygius White-rumped Seed-eater M-P&G 1458 Category (3).

Region A. 'nesting in swallow's nest in VII'

Serinus dorsostriatus White-bellied Canary M-P&G 1449 Category (7) 27 records.

Breeding mainly in the long rains, with 14/17 Region B records March-June and 6/8 Region D records April-June. Both Region C records are from Narok.

Serinus donaldsoni Grosbeak Canary M-P&G 1452, 1453 Category (4) 4 records.

Region D. III, 1; VI, 2; IX, 1 . . . 4

Serinus sulphuratus Brimstone Canary M-P&G 1450 Category (8) 63 records.

The ill-defined breeding seasons of this large canary may result from its variable diet of young shoots and buds of trees and shrubs as well as insects and seeds. According to Skead (1960) this species is more prone to a fruit diet than are other South African canaries. The prolonged late rains, dry season and pre-rains breeding season March-September (28/30 records) in Region C peaks in March, May and August-September, whereas Benson (1963) noted a peak of breeding activity in the hot pre-rains months of August-October elsewhere in the southern tropics, with seasons less defined than in other canaries.

Serinus canicollis Yellow-crowned Canary M-P&G 1454 Category (7) 26 records.

A pronounced long rains peak in Region D May-June (14/23 records) in an otherwise prolonged season. The Region A records are from Mau and Mau Narok at 2700 m, against 2000-2300 m in Region D, and are indicative of after-rains breeding. But Sessions (in litt.) recorded this locally ubiquitous species breeding in all months (nesting or feeding young) at Mau Narok with peaks of breeding activity April-May and October-November, at the beginning of the rains and the beginning of the dry season.

Serinus koliensis Papyrus Canary M-P&G 1451 Category (4) 5 records.

Region B. IV, 1; V, 1; VI, 1; VII, 1; VIII, 1 5

Serinus citrinelloides African Citril M-P&G 1462 Category (8) 60 records.

Breeding in and around the long rains in Region B and both rains in Region D. These April-June and December peaks in Region D are equally evident at Arusha and Nairobi, especially April-June with respectively 9/16 and 10/15 records. Region C records are late in the rains.

Serinus striolatus Streaky Seed-eater M-P&G 1461 Category (9) 171 records.

Region A records are from above 2700 m, where most breeding is July-December (17/21) in the late rains and early dry season. There are Region D records for all months, peaking in the long rains April-July (101/150). Unbiassed records from the vicinity of Nairobi are mainly April-July (37/56) and November-February (18/56), peaking in May (12) and June (12). Biassed Karen records peak in April (20/46) and May (12/46). Arusha records are confined to January-July and October, peaking January-February (8/17). An analysis of records from above 2200 m shows a peak in the long rains in April-July (11/19). It is difficult to draw firm conclusions on the breeding seasons of this often ubiquitous highland species, except that the long rains are favoured for breeding in Region D, with a secondary peak in and after the short rains. High altitude breeders probably avoid the wettest months in Region A.

Serinus burtoni Thick-billed Seed-eater M-P&G 1462 Category (4) 3 records.

Region D. V, 1; VIII, 1; X, 1 . . . 3

Serimus reichardi Stripe-breasted Seed-eater M-P&G 1456 Category (4) 4 records.

Serinus spp. breed mainly in the rains, especially in the long rains; sulphuratus (prone to a fruit diet) has ill-defined seasons; the well documented striolatus favours the long rains in Region D, with a secondary peak in and after the short rains, and high altitude breeders probably avoid the wettest months in Region A (not in Region D).

Discussion

I. General considerations

We feel that we should preface our discussion of breeding seasons (in relation to climatic regimes based chiefly on rainfall and other possible factors) with a quotation from H. L. Mencken, for which we are indebted to Dr Dean Amadon: 'For every complex situation there is a simple explanation, and it is wrong'. We would also quote the late Professor A. J. Marshall who (in discussion with L.H.B. in 1964 on the subject of the conflicting views of D. Lack and V.C. Wynne-Edwards) observed that it was absurd to suppose that any one theory would explain every possible combination of facts. In other words, any situation may have to be examined as a separate entity, evaluated in the light of available facts, and should not be expected to conform infallibly to any particular theory. Lacking adequate facts, speculation can be profitless, even misleading; so can an individual's interpretation of facts and his selection of examples to support a favourite theory.

In an effort to obtain more precise factual material to support some of the broad generalisations made in this paper, especially in relation to plant phenology and abundance of various foods, this Discussion was circulated to a number of authorities in East Africa, requesting comments. They included H. Lamprey and M. D. Gwynne, with special reference to plant ecology; A. W. Diamond, J. F. Reynolds, G. Backhurst and other ornithologists in East Africa; C. R. Cunningham-van Someren, A. Duff Mackay, and M. Clifton of the National Museum, with special reference to ornithology, herpetology, and entomology respectively. A copy was also taken to the Edward Grey Institute at Oxford and, through the Director, C. M. Perrins, circulated inter alia to P. Lack and M. J. Coe. Valuable critical and constructive comments have been received from A. W. Diamond, H. Lamprey, and J. F. Reynolds; and briefer comments from G. R. Cunningham-van Someren, A. Duff Mackay, and M. Clifton, not necessarily on the subjects of their special expertise alone. Some brief comments have also been received from C. M. Perrins. Where these comments have made a useful addition to the discussion section, they have been acknowledged, as, for example, 'Reynolds, pers. comm.'

2. Earlier Relevant Work

The whole of one issue of Ibis (Vol. 92. No. 2. April 1950) was devoted to a discussion on breeding seasons of birds. It contained articles by A. Landsborough Thomson, D. Lack (two), R. E. Moreau (two), A. F. Skutch, and K. H. Voous-the last three on tropical regions. It was the most comprehensive review of the subject, in different parts of the world, up to that time. In the first of two articles in that issue, Moreau (1950) (i) discussed only land birds in Africa; but also (ii) contributed an article on seabirds. Since he covered the whole continent rather than only one region, and since he had far less detailed data available than we have, his treatment was necessarily more general. Moreover, it was influenced by his own personal experience at Amani in Tanganyika (Tanzania). For the ecoclimatic region concerned (our Region D), Amani is in a somewhat unusual environment in that it is in submontane or tropical rain forest with a high rainfall, whereas most of this region is savanna or more arid vegetation types. Moreau was also inclined to draw rather too sweeping conclusions from a small number of records, establishing a 'breeding season', in some cases, from less than five records. On raptors (Falconiformes and Strigiformes) he generalised that they bred chiefly in the cool dry season-a view in some cases erroneous but nevertheless repeated subsequently, unvaried, by many

later authors. Lacking good quantitive data related to climatic patterns and ecology, Moreau recommended that future workers should concentrate on these aspects. Undoubtedly, had he had such data available, he would have modified some of the conclusions he drew. Here we endeavour to meet that need.

Lack (1954) included a chapter on breeding seasons in his book The natural regulation of animal numbers. He also covered the subject more briefly in a later work (Lack 1968) showing that he had not basically altered his views between 1954-1968. His views have often tended to be accepted as the definitive ruling on factors controlling breeding seasons. In his 1954 work, most of the discussion on breeding seasons (in animals, in general) is centred on birds. However, although most bird species are tropical, most of the examples Lack cited are from temperate regions, especially Britain and Western Europe. Partly, this was due to the unavailability of good quantitative data from tropical regions (although, somewhat surprisingly, he made little use of a review of breeding seasons in Central America (Skutch, 1950) which often supported his main hypothesis).

Lack had very little tropical experience (Lack, 1973). Apart from one summer holiday spent at Amani, with Moreau, and a short period spent in the Galapagos Islands (a somewhat aberrant part of the vast tropical regions), his experience was almost entirely in temperate Europe. On occasion, he also tended to misquote, misinterpret or overemphasise aspects of other published work. For example, referring to the White-rumped Swift, Lack observed that 'in Central Tanganyika, where the warm conditions last longer' (our italics) 'these swifts rear three broods a year'-as if they were directly comparable to the Common Swift Apus apus and Pallid Swift A. pallidus, respectively temperate and subtropical species which rear one and two broods in the northern summer. He apparently ignored Moreau's (1942) own puzzlement that the Whiterumped Swift should have such a definite breeding season at Amani where day-length and temperature vary little throughout the year and where there is no question of the warm condition 'lasting longer.' Unlike winter in temperate or subtropical regions, temperature at Amani is not a limiting factor, though other adverse climatic conditions may

operate. Concerning the Little Swift, and apparently on the basis of scanty, inconclusive observations by Pakenham (1943), Lack states that it has two separate breeding seasons in Zanzibar. His review, at least as related to tropical species, is therefore of rather limited value for our purposes. A later and more thorough review, incorporating much tropical data, is that of Immelmann (1971; Chapter 8, in Farner & King, Vol. 1). In his discussion Immelmann mentions that, in several tropical forest regions, restricted breeding seasons have been found, whenconsidering Moreau (1950) at Amani—the contrary might be expected because of the equable climate; and he observed that 'the reasons for these restrictions are not understood'. We agree; and we consider that this is still the case.

Suggestions made by Immelmann are followed by our comments below:

- (i) 'Inhabitants of lowland forests with very heavy precipitation tend to concentrate breeding in the dry months.' While there are no forested regions in East Africa with very heavy precipitation, our data show that in forested areas with annual rainfall of 1500–2500 mm, a great many species breed in the wettest part of the year; so that, in East African conditions, this generalisation is incorrect.
- (ii) 'Most birds... with a regular change between one long dry and one long wet season per year... breed around the rainy season, with only a few specialists laying during the dry period.' Our data largely (but not entirely) bear this out.
- (iii) 'In areas with two wet seasons, various species tend to breed twice a year, whereas others nest in the short rains, but avoid the long rains'. We assume that, in using the terms 'short rains' and 'long rains,' Immelmann means that birds avoid breeding in the wettest months of the year. Although this supposition is supported by several other studies (referred to later), it is not upheld by most East African data, except from eastern Tanzania. In most of Regions B and D, with fairly well-defined bimodal rainfall peaks, the long or heaviest rains of the year are preferred, while some species do breed—more or less proportionately—in both seasons.

For East Africa, then, Immelmann's generalisations on the breeding seasons of tropical birds are thus by no means valid, especially regarding species of the tropical forests and those in bimodal rainfall regimes. On the subject of species breeding in both rainy seasons in bimodal rainfall regimes, he suggests that this can either be due to the same individuals breeding more than once in a year, or to different individuals breeding in each of two rainy seasons. He suggests that bi-annual breeding has only been proved in one species, the Southern Black-backed Gull Larus dominicanus. Recently, however, it has been shown to occur in ringed individuals of Reichenow's Weaver (C. van Someren 1976) and other species at Karen, Kenya; and from available data, there may be deduced the very strong presumption that it occurs also in the African Pied Wagtail (Donnelly 1978) and in the African Rock Martin (Brown, pers. obs.) in Regions E and D respectively.

Immelmann, too, sometimes misquoted or misinterpreted his sources. Discussing under 'Food Supply' ultimate factors controlling breeding seasons, he quotes Brown (1971), to the effect that vultures and eagles of tropical regions breed almost exclusively in the middle of the dry period, when ground cover has largely died off and prey for the young is most easily accessible. This view was generally stated in Moreau (1950); but both in Brown (1952) and Brown (1971) that author is at pains to point out that, when the cover is least and prey easiest to catch and when young are in the nest, the theory does not always apply—sometimes, in fact, the reverse. The behaviour of female adults at nests and their share in providing food is also important. Further discussion will be found later in this paper.

Other authors, e.g. Diamond (1974), Fogden (1972), Maclean (1971), Perrins (1970), Skutch (1950) and Voous (1950) have contributed reviews of seasonal breeding of birds in tropical areas. Those of Diamond, Fogden, Skutch and Voous concern mainly tropical evergreen or forest areas of high, or very high, rainfall; Maclean deals with the arid Kalahari sandvelt; and Perrins deals with temperate species and some seabirds. The very high rainfall tropical forests of Sarawak (Fogden 1972), Indonesia (Voous 1950) and Central America (Skutch 1950) are not really similar to most parts of East Africa, though parts of Jamaica (Diamond 1974) may be more alike, and conditions in the Kalahari sandvelt (Maclean 1971) are clearly nearer those of arid

parts of northern Kenya than those in any of the other areas discussed.

Maclean found that the Ostrich, raptors, nightjars, cuckoos and two passerines (the Capped Wheatear and the African Rock Martin) were seasonal breeders, irrespective of rainfall. Of these, only the Ostrich and raptors were resident, the others intra-African migrants whose breeding season was accordingly connected with their migratory pattern or that of their hosts (cuckoos). Coursers (the Two-banded Courser) bred continuously, independent of any environmental influence and all other species were opportunistic breeders, depending on rainfall. Some insectivorous species began breeding before rain; but seed-eating species generally had a more restricted breeding season following rain. Exceptions to this general trend occurred among doves and sandgrouse, which had more protracted breeding seasons than other seed-eating species. Since Columbidae feed their young on crop secretions, this might have been expected, in their case, but not in sandgrouse. Almost two thirds of Maclean's records, however, concern the Social Weaver Philetairus socius; and the 'season' of some species depends on only one or a few records.

Comparing these data with East African records, many small doves do have protracted breeding seasons, but generally show slight or discernible peaks. Sandgrouse in East Africa have clearly defined peaks, with short breeding seasons in dry weather. Thus, although there are ecological similarities between the drier parts of East Africa and the Kalahari, the same factors evidently do not always operate in the same way for the same families in different areas.

Fogden (1972), working in the very equable, extremely high-rainfall (4000 mm/yr or over) forests of Sarawak, found that—despite the lack of sharp seasonal variations in climate—the main breeding season of birds was quite clearly defined, from December to June, the period when maximum leaf production occurred and insects were most abundant. This applied to both insect-eaters and, more surprisingly, to fruit-eaters also, perhaps because of the need to provide protein-rich insect food for nestlings. Despite the obvious differences between the tropical lowland forests of Sarawak and most parts of East Africa, there are many unexpected

similarities in the clearly-defined breeding seasons, notably among insectivorous passerines in the most equable of our climatic regions, Region B.

In Sarawak, however, there is only one season of the year, in November, when insects are least abundant, correlated with minimum leaf production, and when breeding is reduced. In East African bimodal rainfall regimes, there should be (or are) two such 'lean' seasons, just before each rainfall peak, when leaf production is minimal and consequently supplies of insects should be low. This should be more striking in woodlands or grasslands where the trees are deciduous and grass may be or is entirely consumed by firc. In some areas with bimodal rainfall peaks, notably in Region D, there are two peaks of flower, fresh leaf, and nectar production dependent on the sharp alternation between dry and wet seasons. If insect productivity is directly related to the amount of fresh leaf available, then there should clearly be two peaks of breeding by insectivorous birds. Fogden's main conclusion was that birds should breed whenever their protein level was adequate—that is, when insects increased in abundance, early in the rainy season. In many East African environments, notably the woodlands, grasslands, and thornbush which cover most of our area, insects and protein supplies (enabling birds to breed) should increase twice a year-and, in fact, do.

However, although some birds do breed in both rainy seasons, the majority of forest, woodland, and grassland insect-eaters breed in only one. The available evidence thus indicates that many species of birds with short breeding cycles (and, theoretically, able to breed twice a year) do not actually do so. The effect of seasonal change in available food supply is therefore not always the same in different parts of the world.

Diamond (1974), working in a climate with total rainfall more similar to East African conditions but nevertheless basically a lowland tropical forest environment, found that most birds in Jamaica breed in the Spring (April-May) rains, but that there was little or no nesting in the heaviest rains, August-November. He compared this situation to that at Amani (duplicated also in some other areas of eastern Tanzania (Moreau, 1950, Beesley 1973)), where most breeding occurs in the short rains but not in the main or long rains (April-May). The

Jamaican work was done in a rainfall of 880-2760 mm/yr, so that the total annual rainfall was not greater than in parts of Uganda or at Amani (with rainfall about 1926 mm/yr). Diamond's basic conclusion was that the wettest parts of the year were avoided by most birds for breeding. However, from most parts of East Africa with bimodal rainfall peaks—apart from eastern Tanzania—the evidence shows that most insectivorous birds, whether of forest or woodland, breed most often in the 'long', or main, rains. This particularly applies to our Region B, western Kenya and Uganda, where this result is most surprising.

Voous (1950) summarising Indonesian results obtained in conditions most resembling those studied by Fogden, also found that in Sumatra, Borneo, and Java, birds had distinct breeding seasons despite rather equable, usually wet, tropical climates. This applied to both evergreen and other habitats; but where dry periods were less pronounced (for example, West Java) the breeding activity was lessclearly-defined. The peak breeding months varied, but the breeding period usually started towards the end of the rainy season and reached its peak before the driest month. Thus, in generally equable conditions of high rainfall close to the Equator, his conclusions (based on a total of nearly 4000 records from four main localities) do not accord with those of Fogden (1972), working in rather similar habitat, but with far fewer definite dated records of breeding, though with good data on moult, weight, and insect abundance.

Skutch (1950), who (like Moreau) had the advantage of long residence in his area of study and who, moreover, had carried out detailed life-history studies of many species, concluded that in Central America, at about 10°N and in rainfall of 2500-3000 mm/yr, chiefly in tropical forest, the peak of laying occurred around the vernal equinox, with April the principal month. Rainfall figures, provided for his own estate at El General, show that in his area the peak laying months were in the early rains, as in Jamaica (Diamond 1974); and that the wettest months, August-November, were usually avoided, with only 101/1357 nests, or 7.4% recorded in that time. However, he stressed that the areas he studied were ecologically complex, with many local variations in climate; and concluded that no single climatic feature—such as length or intensity of daylight, alternation of dry and wet seasons, or fluctuations of temperature—appeared to regulate the initiation of breeding.

In several cases, for example among nectar drinkers and birds that fed on insects on the forest floor, the breeding season appeared to him to be directly related to food supplies; and he concluded that April-June was the most important breeding season because food supplies-both vegetable and insectwere then most abundant. Seed-eaters tended to nest later than most birds, correlated with abundance of grass seed. In certain species with peculiar diets, available food supply could dictate breeding at a season climatically inimical. For instance, some hummingbirds reared young when nights were frosty; and small ground feeders nested in seasons of chilly, drenching rains. In fact, Skutch produced strong support for the theory that food supply ultimately controlled breeding seasons, but suggested that many birds might have an internal physiological rhythm which enables them to reach a state of readiness to breed, after which they could be 'triggered' to lay by a stimulus, such as the onset of the rains.

Perrins (1970), dealing largely with temperate species and seabirds, suggested that food supply for breeding females might limit their ability to lay at a time which would be optimal for rearing the young hatched from those eggs. Not all species are likely to be so prevented from laying at times which would be most advantageous for rearing young, the groups most affected being small species laying large clutches relative to their own bodyweight. In most tropical species, clutches are smaller than in temperate species, though food supplies may seem more abundant. In his comments on the discussion section of this paper, Perrins observed 'the message of my 1970 paper is that one cannot guess what part of even a short season is best without making fairly detailed measurements' (of several different parameters, presumably, including environmental factors, and not only of the birds themselves). His suggestions on factors controlling the breeding season do not fit East African results, either.

Thus, study of available recent literature, and of reviews by Lack (1954, 1968) and Immelmann (1971) indicates that there is no clear consistent

pattern in the breeding of tropical birds, and that therefore any generalisations are at present unsound. In two tropical American regions (Diamond 1974, Skutch 1950) most breeding occurs in the spring rains, the wettest parts of the year being avoided. In two far eastern tropical regions (Fogden 1972, Voous 1950) most breeding occurs in the main rains, sometimes late in and just after the main rains, with no consistent pattern, even in rather similar rainfall regimes. For East Africa, the tendency has been to assume that the pattern shown by Amani or eastern Tanzania (based largely on Moreau (1950)) is typical, with the heaviest rains being avoided, as in Central America and Jamaica. However, most of the recent results show that, if there are two rainfall peaks in the year, the heaviest rains are preferred, not avoided.

The East African data here presented—from a region which is topographically, climatically, and ecologically extremely complex—provide many examples which conflict with, or contradict, results derived from studies in these other regions, none of which is very like East Africa. Factors affecting breeding in East Africa must therefore be evaluated on their own merits and cannot be expected to conform to theories formulated in other parts of the world, especially in temperate regions where variations in day-length and temperature are more important. In East Africa—and other parts of Africa—the alternation between dry and wet seasons is the most important environmental factor affecting breeding seasons.

3. Proximate and Ultimate Factors affecting breeding Seasons

It is generally agreed that the breeding seasons of birds are regulated by proximate factors, initiating breeding; and ultimate factors controlling success through survival of the young. Subsidiary or modifying factors can halt the breeding cycle after it has started. Proximate factors must obviously come first, but ultimate factors may be more important for survival once the cycle has started (Baker 1938; Lack 1954; Immelmann 1971).

The time gap between the beginning and end of a breeding cycle in East African birds can be from one to nine months. Occasionally, it is longer—for example, up to 22 months in the Crowned Eagle. Probably, the longer the breeding cycle, the greater the risk of a subsidiary or modifying factor affecting its course and ultimate success. Such modifying factors are thus more likely to affect large non-passerine species (with breeding cycles of several months, perhaps spanning parts of both wet and dry seasons)—than a small insect-eating passerine which can complete its entire breeding cycle in a relatively stable, generally wet, or moist, environment. Thus, among several herons, erratic (not necessarily annual) breeding appears to be triggered by heavy rain, or extensive flooding, but can be halted by premature cessation of the rains.

Proximate factors, initiating breeding, are defined (in 'A New Dictionary of Birds' ed. A. Landsborough Thomson, 1964) as 'in a system of causation, that immediately precede the effect—contrasted with ultimate'. Since they come first, they are discussed first here. 'Ultimate factors' are similarly defined as 'factors that are remotely causative, but do not lead immediately to the effect—contrasted with proximate'. Subsidiary, or modifying, factors are not defined in the 'New Dictionary' but are discussed after proximate factors by Immelmann (1971).

For species with long breeding seasons, there must evidently be difficulty in deciding what are proximate and what are ultimate factors. Thus, in Rüppell's Griffon, rainfall which apparently triggers breeding some seven months before the young become independent (Houston 1976) is an ultimate factor, remotely causative, resulting in young being better able to compete with adults when food supplies are at a maximum. The same factors do not always operate equally on the same species. The Ostrich, for instance, has a regular breeding season in perennial grasslands near Nairobi, but is an opportunistic breeder in the Namib Desert (Sauer & Sauer 1966) and could be expected to be opportunistic in arid, northern Kenya. Our data suggest this but are inadequate to prove it.

PROXIMATE FACTORS, as listed and discussed by Immelmann (1971), include:

(i) Endogenous (growing from within) rhythms, apparently principally affecting some seabirds (such as the Sooty Tern) where other environmental conditions are unimportant, and the

timing of breeding is controlled by the period needed to complete a breeding cycle and moult (Ashmole 1962, 1963). The same endogenous rhythm does not affect the Sooty Tern in East African waters, where it breeds erratically—in calm conditions in one known station and rough water in another. Endogenous rhythms are normally affected by environmental factors so that the timing of breeding becomes controlled by exogenous (coming from external sources) factors, the breeding being set in phase by external stimuli. In tropical areas with rather unpredictable climate, many species can remain for long periods with gonads rather advanced, ready to breed, so that they can immediately respond when environmental conditions are suitable (Skutch 1950, Immelmann 1971);

(ii) The Zeitgeber concept (literally 'time-giver' or 'starter'): Ultimate factors affecting survival may be operating most effectively towards the end of the breeding season and, accordingly, too late to initiate gonadal development. However, gonadal development must take place before any eggs can be laid and is initiated by proximate factors, distinct from the ultimate factors which keep the organism adapted in conformity with its environment. The Zeitgeber synchronises endogenous periodicity, initiated by proximate factors, with environmental changes of similar frequency. If such environmental changes occur once or-in areas of bimodal rainfall peaks-twice a year, the Zeitgeber should be related to these regularlyrecurring phenomena. In areas where breeding is irregular or opportunistic, the Zeitgeber would equally be related to irregular improvements in conditions and independent of more regular phenomena connected with the cycle of the sun.

Thus, the Zeitgeber of the Ostrich in the Namib Desert (Sauer & Sauer 1966) must be quite different from that of the Ostrich in Nairobi National Park and other East African grasslands. It could also be different in areas of sharply decreasing rainfall—for example, in Meru district and the areas immediately north with much lower total rainfall, but with

the same basic bimodal rainfall pattern—even though such areas are not far apart geographically. To succeed in breeding at all, the Ostrich must be ready to lay a clutch of eggs when suitable conditions occur. However, such conditions should occur regularly, twice a year, in perennial grasslands (for example, in Meru National Park) and very seldom (not necessarily annually) in areas of subdesert scrub, 50 kilometres to the north.

(iii) Photoperiod: Of critical importance in middle and higher latitudes, north or south, this is generally regarded as unimportant in the near-equatorial tropics (Moreau 1950, Voous 1950, Fogden 1972). In tropical areas, the fluctuations in day-length are small and are not necessarily connected with changes in food supply or other environmental conditions. There may be some slight response to changes in day-length in tropical birds; but other factors are likely to be much more important.

(iv) Rainfall and related factors: Reproduction in many birds, especially in arid zones, is immediately stimulated by rainfall. Whether it is the actual rainfall itself, or whether it is the immediate result of the rainfall in the rapid appearance of green vegetation and improved food supply, is not clear. In species of very arid areas, early and opportunistic breeders must initiate (or complete development of the gonads) well before the increased vegetative cover and food supply, resulting from a wet season, are available. Actual rainfall is normally the earliest environmental factor connected with a forthcoming favourable season and is thus as important, in the tropics, as is photoperiodicity in temperate zones. Variations in local or annual rainfall frequently result in corresponding differences in breeding seasons. Late rains delay breeding, whereas early rains may stimulate early breeding; out of season rains can result in breeding at unusual times of year. In very arid areas, with irregular distribution of showers, breeding may be restricted to areas affected by individual thunderstorms.

In East Africa, and especially perhaps in our Region C, there is a pre-rains flush of leaf and flower-especially noticeable in Brachystegia woodland-which seems to stimulate breeding in some species. Moreau (1950) makes much of the importance of this pre-rains emergence of leaf in woodlands of southern Africa. In a later work (Moreau, 1966), he notes that this pre-rains emergence of leaf on trees and bushes is typical of most tropical African savanna areas, including semi-arid acacia bushlands. Some trees, notably Erythrina and Acacia spp., also flower before any rain falls. This pre-rains flowering and outburst of leaf often occurs in very hot weather, just before the rains; birds that breed in this season cannot be responding to actual rain. Whether they are responding to the appearance of green leaf and flowers as the Zeitgeber, or to high prevailing temperatures which may stimulate the production of leaf and flower, is not clear. Temperature or, perhaps more important, a sharp rise in temperature, is listed by Immelman (1971) as a subsidiary or modifying factor; but, in this case, it could be a proximate factor stimulating breeding to take advantage of newly-available green leaf.

ULTIMATE FACTORS, as listed by Immelmann, include food supply, competition, nesting conditions, predation pressure, and climatic factors. He states that 'every species is adapted to breed at the time of the year when it can raise its young most efficiently'. Gene complexes of those pairs producing young at the 'wrong' time of year will be reduced, or eliminated, by natural selection. Such selection pressure is likely to be greatest in species with specialised feeding, or nesting, habits and which breed in areas where the favourable season is short. Specialists may have a brief and well-synchronised breeding season, whereas non-specialists are less restricted. He cites pigeons and doves, which feed their young on crop secretions, as non-specialist: largely independent of special food requirements for raising their young. This generalisation is not entirely borne out by East African data for-though some pigeons and doves do have extended breeding seasons-they can also show more or less clear

breeding peaks. Specialists, in East Africa, could surely include the Greater and Lesser flamingos, which also feed their young on a crop secretion (Studer-Thiersch 1966); but which certainly do not have either a brief, or well-synchronised, breeding season, being opportunistic and generally irregular breeders, with a total cycle spanning $3\frac{1}{2}$ months.

We now examine these points further:

(i) Food supply:

This is regarded by most authors on breeding seasons as being the most important ultimate factor for nearly all bird species. The greatest demand on available food supply is towards the end of the breeding season, when population density is highest; but great demands are also necessary when the female is producing her eggs and when young in the nest are being fed. However, Immelmann (1971) says that 'each species has therefore evolved its breeding so that it coincides with a maximum availability of its species-specific food'-as if this were an almost or quite invariable rule. It certainly does not fit all species in East Africa. There are cases where other factors apparently, or certainly, override abundance of species-specific food. The African Skimmer, for instance, breeds in the rains on Lake Turkana, but in the height of the dry season on rivers liable to flooding. The Collared Pratincole breeds in the height of the dry season on river rocks liable to be covered by floods and, in the cooler mid-year dry season in the more stable conditions of Lake Victoria. These species feed respectively on small aquatic organisms and on insects aerially caught. All five plains-living Vanellus species-all said to feed on insects, worms, molluscs and other small invertebrates and occasionally on grass seeds-breed in the rains in the drier parts of their range in East Africa, and in the dry season in the wetter parts of their range. Such examples suggest that food-supply is not the overridingly important ultimate factor that it is often claimed to be.

Immelmann goes on to say that most tropical birds exploit the seasonal flush of vegetation and insects during wet periods. Among passerines the first may be aerial hunters feeding on flying insects, followed by species foraging in foliage of trees, then by grass-living insectivores, and ending with seed-eaters, late in the wet, or early in the dry, seasons.

While many of our East African data support this generalisation, by no means all do; and suitable conditions which result in an available food supply do not necessarily mean that birds will breed.

(ii) Competition:

In this connection, Immelmann cites especially the competition resulting from an enormous increase in the bird population of Central and South America, following the influx of northern migrants in winter. In some areas, local residents avoid this season for breeding; among places already mentioned in this discussion, he cites Skutch (1950) on Central America and Maclean (1971) on the Kalahari. However, in parts of East Africa, the precise opposite occurs, notably in those parts of eastern Tanzania where the short rains October-December is the preferred breeding season in a bimodal rainfall (Moreau 1950, Beesley 1973). In this area, this is the time of maximum influx of Palaearctic migrants. However, such possible competition would support the generallyobserved preference among many species for breeding in the long rains, March-May, when the population of Palaearctic migrants is least or they have gone altogether. The 'order of magnitude' numbers of Palaearctic migrants in relation to permanent residents has not been calculated even by Moreau (1972); but this factor may well be much less important than is often thought. It has been estimated by Brown (in press) at about 10-20% of the residents. Locally, some migrants (such as the European Swallow Hirundo rustica and several raptors, such as the European race of the Kestrel Falco tinnunculus and Lesser Kestrel F. naumanni) far outnumber their resident local counterparts. However, in Region A, most raptors breed at a time when the maximum competition from an influx of Palaearctic migrants is likely-that is, between October and March.

Competition may also affect colonial species with limited nesting space—for instance, cormorants on Lake Victoria (Marshall & Roberts 1959) or pelicans (Brown, Powell-Cotton & Hopcraft 1973)—in which successive groups occupy space as it is vacated by earlier breeders. A continuous succession of such groups the year round, such as occurs among cormorants on Lake Naivasha and Lake Nakuru, does not suggest that competition for food is important, though detailed studies have not been done on the

relative breeding success of these successive groups at different seasons.

(iii) Nesting condition:

Many birds breeding in river banks-for instance bee-eaters, swallows, and some kingfishers-nest when the rivers are low and suitable banks are available. Similarly, species breeding on sandbankssuch as thicknees, some plovers and skimmersmust lay when they are not in danger of being flooded out. Grass-dwelling birds (such as Euplectes spp.) begin to nest rather late in the wet season as they must wait for available nesting sites and material. Some birds requiring special nesting materials—for instance swallows which build nests of mud-must normally wait until suitable mud is made available by rainfall. However, at least some such species (for example, the African Rock Martin) can then rear a succession of broods in the same nest, or can use an old nest with little or no repair. In East Africa, the majority of mud-building swallows lay in the rains, when insects are also likely to be abundant, so that, in these cases, more than one factor may be operating on the timing of the breeding season. However, without mud, no amount of insect life would enable these swallows to breed; the onset of the rains and increased supplies of insects resulting therefrom may be secondary to the availability of special building material.

(iv) Predation pressure:

Many ground-nesting water birds in Australia prefer to breed when a rise in water has made islets available. This may also apply in East Africa, at least in some cases. Inaccessibility of the breeding site to disturbance by large mammals (especially human beings) may be the key feature in the varied breeding seasons of the Great White Pelican (Brown & Urban, 1969). Several other species (such as Grey-headed Gulls) breed on inaccessible, or relatively inaccessible, islands; in this case, however, breeding occurs in the main rains or just after, and might be connected with food supply as well as inaccessibility of the islands.

In this connection, Immelmann cites Elliott (1950) on the predatory effects of driver ants. 'Some forest birds of tropical Africa avoid the occupation of nests during the hunting season of driver ants', he says.

While the predatory effect of driver ants deserves more intensive study, in general it seems that small forest passerines, mainly insect eaters, breed chiefly in the height of the rains when driver ants are likely to be at least as active—if not more so than—as at any other time of year.

(v) Climatic factors:

In general it is thought that climatic factors mainly exert an indirect influence resulting in changes in vegetation and food supply. However, low temperatures inhibit breeding in many temperate species. Even in the tropics, a period of low minimum temperatures may lead to a low level of breeding (Snow & Snow 1964). In East Africa, it appears that in a large number of species inhabiting regions with bimodal rainfall regimes and two dry seasons per year, the mid-year (or cooler) of the two dry seasons is preferred. This applies to many groundbreeding species—for instance, plovers, avocets and stilts, coursers, pratincoles, and sandgrouse. J. F. Reynolds (pers. comm.) has suggested to us that this may be connected more with relatively low ground temperatures, resulting from heavy cloud cover and reduced sunlight, than with comparatively small differences in minimum ambient temperatures. Raptors also, given an alternative, tend to select the cool mid-year dry season and this may be connected with a reduced need to spend time on the nest shading the young. However, in areas with only one dry season, raptors breed then. A preference for the cooler, mid-year dry season in Region D may, in some cases, be due more to availability of food than to low temperatures and cloud cover. This is further discussed under 'raptors', later in this paper.

Heavy rains may have a depressing effect and, in the humid tropics, many species tend to avoid breeding in the wettest part of the year (Skutch 1950, Diamond 1974). While this is true in some cases, it is not true in all—see, for example, Fogden (1972), in one of the wettest areas yet studied. In East Africa, where rainfall is not normally as high as in some other parts of the tropics, it appears that among a large number of species the wettest part of the year is actually preferred, or selected, for breeding. Possibly this effect is variable according to the upper threshold of rainfall concerned, being most evident

in tropical forests with more than 2000 mm annual rainfall. Intensity of rainfall is also a factor to be considered. A colony of about 8300 pairs of Great White Pelicans, incubating in July 1977, deserted en masse, apparently because of exceptional storms causing a rise of more than 300 mm in the lake level between 29 and 31 July. Many of the breeding islands would actually have been swamped by rising water and waves; but even the pelicans which were incubating a metre or more above water level deserted (Brown: pers. obs.).

Persistent strong winds may likewise have a negative effect—for example, on two species of cormorants on Lake Victoria, where (according to Marshall & Roberts (1959)) breeding is confined to relatively windless months between late May and December. This view is based upon incomplete data, however, for our records show that cormorants breed on Lake Victoria year-round, at least in some parts.

Which of the proximate, or ultimate, factors mentioned is most important in controlling the season of breeding? The answer may depend on the response to the further question: 'Which comes first, the chicken or the egg'. In terms of timing, quite clearly the egg comes first, sometimes many months before the chicken. If females cannot form eggs because of lack of protein for example (Fogden 1972), then no breeding can occur. In such a case, the proximate factors controlling development of the gonads could be expected to override ultimate factors (which would otherwise stimulate breeding, or permit it to take place). If, however, conditions are favourable before the breeding season, and gonadal development proceeds normally, laying may be followed by a period of food shortage, so that young cannot be successfully reared. In that case, the ultimate factor of food supply during the nestling, or post-fledging, period would operate to control breeding success. Evidently, in conditions of erratic rainfall and widely-varying food abundance-a situation typical of much of East Africa-either of these possibilities might occur; but they should be less likely in relatively equable conditions, such as forests, than in extremely arid areas where opportunistic breeding may be the rule. Immelmann (1971) has pointed out that, where opportunistic breeding occurs, the birds must have been ready to reproduce

sometime before adventitious good rains suddenly created favourable conditions and suddenly improved the ultimate factors affecting breeding success (including availability of nesting sites and food supply).

Many authors, notably Lack (1954, 1968), have considered that, of all possible factors controlling the breeding season, food supply is of overriding importance. This view is also stated by Skutch (1950), Immelmann (1971), Fogden (1972) and others, though Moreau (1950) and Voous (1950) are more cautious. Moreau, having considered a wide variety of parameters (such as rainfall, day-length, temperature) and visual stimuli (such as grass fires), considered that there was no single stimulus of overmastering importance initiating breeding seasons. Different species, or even the same species breeding in areas not far apart, could be stimulated to breed by different climatic or other factors. Our data reinforce this perceptive conclusion and, where adequate, show that—even in the same species—different stimuli may affect the breeding rhythm in different areas, geographically close together but ecologically different. In some areas, a species may breed in the rains; in others, not far away, in the dry season. Many large water birds—for instance, herons, pelicans, flamingos, and storks-breed very erratically and irregularly, laying in numbers in one year, and not at all in others. There is often no obvious explanation for these irregular phenomena, which cannot be closely related either to food supply or climatic factors. Skutch (1950) suggested that, in tropical-forested Central America, mainly between 5-15°N, internal physiological rhythm enabled many birds to reach a state of physiological readiness to breed, after which they could finally be triggered to lay by a stimulus such as the onset of the rains. Moreau (1950) had come to a somewhat similar conclusion related to the Zanzibar Red Bishop in northern Tanzania; and Marshall & Disney (1957) have shown experimentally that the appearance of green grass blades triggers nestbuilding by male Red-billed Quclea. While there are many examples among our data—especially concerning small species —to support this hypothesis, it does not explain all the phenomena observed.

Lack (1954), working mainly or entirely with temperate species, held the view that every bird

must breed every time it can-that is, wherever a breeding site and a food supply is available. He also maintained that birds would lay as large clutches as they could and that brood size and success was primarily determined by clutch size. He maintained (in discussion with L.H.B., in 1961 on the subject of non-breeding among large tropical raptors) that there could be no such thing as a true nonbreeding pair—that is, a pair with secure breeding site and adequate food supply which yet did not lay-contending that, in all such cases, detailed study would reveal that the cause was inability to provide enough food. In a later work (Lack, 1968), he stated that 'whereas environment permits a species to raise more than one brood a year, it tends to start breeding as early as possible even though the time at which the first brood is raised is less favourable than later on, in order to fit in as many broods as possible', and later '.... where only one brood is possible, laying will be timed so that young are in the nest in the most favourable period for feeding them 'He added that this last statement required modification but cited only temperate species such as the Great Tit Parus major, Common Swift Apus apus, Pied Flycatcher Ficedula hypoleuca, Cuckoo Cuculus canorus and Manx Shearwater Puffinus puffinus. He believed that every bird should breed as often as it could, lay as many-and as large—clutches as it could and rear all the young it could. Apparently he disregarded the fact that the end result was wasteful in that more young would be reared than could possibly survive. Whether, in the light of more extensive tropical experience, he would have modified these views, cannot now be known. However, if such views were logically applied to East African conditions, every species would attempt to breed every time nesting site and food supply were available, and would rear as many broods as possible. Data collected in this paper suggest that, while the availability of a breeding site and a food supply may be prerequisites for successful breeding, the converse—that the availability of food and breeding site will necessarily initiate one or more breeding attempts during the year (as Lack apparently believed, and certainly implied)—is incorrect.

Availability of a breeding site and a food supply does not necessarily result in a breeding attempt.

Moreau (1950) noted that it was most surprising that, in relatively equable tropical conditions, birds should have—as many do—very restricted breeding seasons. Specifically he cited Shelley's Greenbul with several pairs laying on the same day; and found it puzzling that the Silvery-cheeked Hornbill should have a restricted breeding season, when some fruit supplies were available the year round (Moreau 1936). Among our own data, it is clear that, even in equable forest conditions, many small passerines breed in one of two available rainy seasons, not always the same, the short rains being preferred in some areas, but more often the long or main rains. If Lack's theories (to the effect that every bird breeds whenever it can—and as often as possible in a breeding season) were applied to East Africa, some breeding should occur whenever food supplies and breeding sites become available, in each of the rainy seasons. Selection of one wet season in preference to another is particularly remarkable in our Region B, climatically the most equable of all our eco-geographical regions. Here, most small birds tend to breed in the long, or main, rains. Our data here largely contradict (though they also include) the most limited records available to Moreau (1950) from near Entebbe.

It might be argued that breeding in both rains is physiologically impossible. However, this would be difficult to believe when, in temperate climates, similar-sized passerines can lay more than one-and usually larger-clutch and rear more than oneusually larger-brood in a year than occurs in East Africa. Fogden (1972) suggests that the reason for this is the relatively small 'order of magnitude' increase in insect life in Sarawak forests compared to temperate forests (three- or four-fold as compared to several hundred fold). There is, of course, an obvious difference between temperate conditions (when virtually all insect life is dormant in winter and relatively very abundant in summer) and those of an equatorial forest, where some insects are available year-round. Although the quantitative evidence of insect abundance in bimodal rainfall regimes in East Africa is apparently rather limited, it tends to show (as discussed later, under Seasonal Food Abundance; Insects) that an expected increase in insect abundance occurs in both rainy seasons. There is a marked and restricted preference, however, for one of two available rainy seasons among many

insectivorous birds—a preference not explained by either the proportionate availability of food supply or inability to breed several times in one year. Some species do show breeding peaks broadly proportionate to expected variation in food supply; others can breed several times in one year.

Moreover, our data show that in such widely diverse birds as the Crowned Crane, the Little Swift, the Golden-rumped Tinkerbird, the Pied Wagtail and the African Rock Martin, a succession of clutches may be laid and broods reared (up to eight attempts in 12 months with the Pied Wagtail) within a year, one brood following immediately upon another, or following a failure. Successive broods have also been recorded in the Malachite Kingfisher (Reyer, unpub.) and in two turacos (Candy, unpub.), while even in a very large raptor, the Crowned Eagle, the same female laid in December—an abnormal time of year—following on her failure to rear a young bird to independence (Brown 1966). These cases support Lack's theory that every bird must breed whenever it can and rear as many young as possible—but they are exceptions rather than the rule.

This theory (termed by Skutch (1967) the 'theory of maximum reproduction') has been questioned by him as applicable to the relatively-stable conditions of tropical forests. 'Maximum reproduction' might be of advantage, however, in temperate areas, where a severe winter for instance, could produce catastrophic losses and, to ensure the survival of a species, could necessitate the most rapid possible reproduction by the most prolific genotypes in subsequent years. Skutch propounded instead a 'theory of adjusted reproduction, in which species would produce only enough young to balance their annual losses. In many cases, 'maximum reproduction' would produce far more young than the habitat could support, and the excess would die of starvation, disease, or be killed by predators. In adjusted reproduction, the reproductive rate is determined by the annual mortality; and birds do not rear more young than are required to balance that mortality. This theory would better explain the apparentlyrestricted breeding of many East African specieswhen nesting sites and food supply are apparently available and when they could breed but do not--than does the theory of maximum reproduction. However, in very arid conditions, where catastrophic losses are likely (as in northern winters) maximum reproduction when possible may be necessary and desirable. Species in our area which might be so affected include the nomadic Harlequin Quail, the Wattled Starling and the Fire-crowned Bishop, though the few accurately-dated records we have do not adequately reflect the true numbers of breeding pairs involved.

We can make no full attempt to determine which, if any, of the proximate or ultimate factors affecting the timing of the breeding season is overriding in the very varied climatic and ecological conditions of East Africa. We agree with Moreau (1950) that no single stimulus is of overmastering importance. In assessing the situation, we are also hampered by the lack of good, detailed studies on breedingbehaviour, on the food taken by many species, and by the lack of good quantitative data on such subjects as the production of green leaves, flowers or nectar. Botanists avoid the subject of plant phenology (dates of production of leaves, flowers and fruits) owing to the varied and often localised climatic conditions prevailing within East Africa (Gillett pers. comm.); zoologists must then attempt to provide such data for themselves. Further discussion is found under individual species (where records are adequate) and later in this paper, for groups feeding on similar foods or inhabiting similar habitats.

However, from our data, it appears to us that the following tendencies are discernible:

- (a) Many (if not most) birds in East Africa do not breed as often as, theoretically, they could. A very large number—the majority of small species and some large—breed in one of two rainy seasons, though conditions apparently suitable for some breeding may occur in both (with some available food supply and a nest site). The fact that several species of similar habits do breed in both of two available rainy seasons reinforces the likelihood that others could but do not.
- (b) In Regions A and C(with clear-cut six-monthly dry and wet periods alternating), breeding seasons tend to be more clearly-defined and related to dry or wet conditions, though our records are generally inadequate for both these regions. Here, as in temperate climates, a succession of proximate and ultimate factors following closely upon one

another may result in more regular breeding seasons.

(c) In many cases—for instance, in species breeding on river sandbanks or banks, or on ground liable to flooding or waterlogging—ultimate factors selecting for breeding at these times (but dependent on climatic conditions rather than food supply) appear to be overriding in timing the breeding season. In some such cases, for instance in swallows, the immediate trigger of availability of mud for nest builiding may be closely followed by a more abundant food supply. In others, it seems that food supply must either be relatively unimportant, or adequate whenever the species concerned can breed, or becomes more abundant some time later.

4. Seasonal availability of Food Supplies

Discussion on this subject necessitates an attempt to summarise available knowledge on the seasonal abundance of food supplies. If food supplies are as all-important in the timing of breeding seasons as is often claimed, then we must know what they are and when they are available. Discussion is hampered by the fact that, in a good many species, critical studies of breeding behaviour and food taken have not been done; nor are there adequate quantitative data on food taken by adults before breeding or by young after fledging (Cunningham-van Someren, pers. comm.). Any discussion of breeding seasons in relation to food supplies must often be based upon rather scanty facts, or upon well-founded generalisations that a particular species feeds upon insects, fruit, or some other available supply. In a few groups, notably among large raptors and some storks, it is possible to relate breeding seasons rather more precisely to available food supply; but equally there are many cases where available evidence makes it impossible to correlate food supply with breeding seasons.

Discussion on seasonal availability of foods may conveniently be divided into (a) primary productivity of vegetation and (b) seasonal availability of certain vegetable, or animal, foods. The second is often—but not always—directly related to the first. Evidently, too, over a vast and varied geographical region such as our Region D (in which rainfall varies from less

than 200 to over 2000 mm/yr, altitude from sea level to over 6000 m, and temperature from permanent glacial cold to over 35°C), vegetative productivity varies in almost infinite degree, although over the whole area the basic rainfall pattern (with bimodal rainfall peaking April–June and November–December) is similar.

(a) Primary Productivity of Vegetation: Although much general knowledge is available on the behaviour of plants in response to climatic conditions, there is usually very little specific or quantitative recorded data. The same applies to foods-such as insects, or nectar directly derived from, or dependent upon, vegetation of one kind and another. Broadly, however, within our area, a cline of increasing productivity of vegetation is related to increase of rainfall, from desert with small shrubs and adventitious annual plants to tropical forest, 50 m tall or more, and always green. Small exceptions to this generalisation occur on high mountains where low temperatures become a limiting factor. For a fuller modern description of East African vegetation, related to variations in available moisture, see Pratt & Gwynne (1977).

At any rainfall level, the vegetation may locally be affected by topography, soil type, drainage pattern, and especially human interference, including that caused by domestic stock. It very often occurs naturally in a regular succession, or catena, based on soil type and drainage. Thus, in much of eastern Uganda, tropical forest alternates with Papyrus Cyperus papyrus swamp; and in broadleaved woodlands of Regions A and C (and elsewhere), welldrained ridges of sandy or loam soil, dominated by such trees as Brachystegia, Julbernardia, Terminalia and Combretum, alternate in gentle undulations with poorly-drained valleys and basins with heavy clay soils, usually supporting more open grassland, and with some specialised trees such as Acacia seyal and Phoenix palms. Bird communities associated with particular vegetation types can vary substantially within I km or less, though evidently the total amount of rainfall and its distribution can scarcely vary much in the same distance.

Some attempt at simplification of the situations is necessary; and, for our purposes, we define five widespread vegetation types, excluding specialised habitats such as rivers, swamps, and bare rock, which can occur in any rainfall region. These are: (i) Forest, mainly submontane and tropical; (ii) Broad-leaved savannas and woodlands; (ii) Acacia savannas and grass plains; (iv) Thornbush or bushveld and (v) subdesert scrub and desert. Apart from forest, which is usually sharply-divided from broadleaved woodland (though in parts of Tanzania there is more gradual transition from Brachystegia woodland to forest), the main types intergrade gradually with one another, very often in a mosaic affected by the drainage patterns. Moister vegetation types persist along drainage lines into areas of lower rainfall. The main characteristics of these broad-vegetation types areas follows:

(i) FOREST: Characteristically, it is composed of tall, woody species, up to 50 m high, producing a layered leaf-canopy which excludes most of the incident light from the forest floor. Typically, there is an upper canopy of tall emergents; an intermediate layer of leafy understory trees and saplings of the emergents; and some shrubs on the forest floor. Only about 1% of the incident light may reach the forest floor, so that primary productivity of vegetation at this level is low, despite abundant moisture. Very little grass occurs among the shrubs. In undisturbed forest, fires do not normally occur naturally and are difficult to ignite.

Most of the available nutrients in the forest ecosystem are locked up in standing timber; so that, despite the high rainfall and generally high temperatures, the amount of green material produced annually may possibly be less than that produced in woodland or grassland with lower rainfall. While we have not been able to locate a precise measurement of the weight of green leaf produced by a tropical forest in East Africa, it is clear that some green leaf, flowers, and fruit are available year-round. This may be reflected in the amount of insect food available year-round, although this varies at least substantially according to season. The forest leaflitter provides food for certain species (for instance, the African Pitta, and several turdids) and dead and rotting wood harbours boring insect larvae.

However, at least in the Nairobi area, very marked seasonality of green leaf or fruit production may not be plainly evident. Some trees such as *Schrebera elata* vary considerably in their period of producing

green leaf—one being in full flush while a neighbour, a few metres away, is naked. Similarly, two adjacent. fig trees of the same species may fruit at different times of year, though only a few metres apart (L.H.B. pers. obs. and C.-van Someren, comments). Productivity, both of leaf and fruit, also varies from year to year. Seasonally, fruit is more abundant in certain species, producing a greater weight of eatable material than either leaf or flowers. Again, there seem to be no precise figures; but some of the large forest fig trees individually produce tons of fruit, which may be the staple food not only of many bird species but of troops of large mammals, such as baboons *Papio anubis* and monkeys *Cercopithecus* spp.

Climatically, the forest is the most equable of all vegetation types—perennially leafy, with little wind under the upper canopy and temperatures varying little from month to month. However, during the rains, the interior of the forest becomes soaking wet; and because of the low evaporation rate within the tree cover and the relatively low incidence of sunlight, it remains wet, or moist, long after adjacent savanna would have dried out following rainfall of similar intensity.

Most forest trees are more or less evergreen, losing some of their leaves in dry periods, and producing new leaf just before and early in the rains. Their response varies locally according to the severity of the dry periods and the amount and intensity of subsequent rainfall. Maximum leaf-growth occurs from early in, to the middle of the rains; the maximum amount of leaf being late in the rains, or just after they cease. However, the individual performance of particular trees of the same species in the same forest varies quite widely, so that fresh green foliage may be available for several months. Many forest trees also flower just before, or early in, the rains, resulting in a flow of nectar, and a supply of small insects attracted to flowers.

As pointed out by Moreau (1936) at Amani, some fruit is available year-round. However, most forest trees produce fruit in the dry season, often the hottest time of the year. Some forest trees such as *Trema* spp. produce some fruit year-round, but most copiously in the hot, dry season, when leaf growth has stopped. Other trees may only be in fruit at other seasons. Large, mobile forest birds

(such as pigeons, turacos, hornbills, and starlings) are able to take advantage of such locally-abundant supplies. Smaller, skulking species of the undergrowth—such as greenbuls, which may also be territorial, and so unwilling to leave a particular area—are less able to do so. Assessment of the food supply available to bird species thus depends not only on the actual primary productivity of the environment but upon the individual foraging habits and ability to secure more distant supplies shown by bird species themselves.

(ii) WOODLAND AND**BROAD-LEAVED** SAVANNA: The boundary between forest and woodland, or savanna, is usually sharp with no gradual cline from the forest environment to the much lower (seldom exceeding 15 m) savanna or woodland vegetation. Forests are usually separated from woodlands by a screen of shrubs and creepers and are frequented by certain birds known as 'forest edge' species. In woodland or savanna, the components of the vegetative layer are: (a) a canopy of usually less than 50% broad-leaved, fire-resistant deciduous tree species, normally less than 15 m tall; (b) a shrub layer which, unlike that within forest, is frequently killed down to the rootstock by grass fires; and (c)-most important-a ground layer, composed mainly of perennial grasses, usually tall and tufted, up to 2 m high, such as species of Pennisetum, Hyparrhenia, Beckeropsis, Panicum, and Setaria.

The amount (and precise species) of grass present depends upon many factors, such as the soil type, total annual rainfall and its distribution. Broadly, the productivity of the grass increases in direct relation to the rainfall and decreases with increase in tree cover. Suppression of grass fires, over several years, leads to increased density of the tree and shrub layers, and consequent reduction of grass. When grass fires cannot sweep through the woodland with sufficient heat to suppress trees and shrubs, a climax woodland condition may result. A Kenya example of this is the *Brachystegia* woodland in the Arabuko-Sokoke Forest near Malindi, Region E.

On the other hand, human interference, in the form of cultivation (when trees are lopped, or felled, and subsequently burned) leads to more open woodland, often in patches with grass the dominant vegetative component. Grasslands of this type (which may also occur in areas formerly dominated by tall forest) bear little coherent relation to the soil type, drainage pattern or topography but are scattered in a random manner over the landscape and are known as 'derived grasslands' (Vesey-Fitzgerald 1974). Usually, they support typical grass-loving insectivorous or seed-eating birds.

In the absence of a dense tree cover, the vigour and productivity of the perennial grasses is related to the amount of rainfall. It may vary from well over 100 metric tons/ha/yr in rainfall of over 1500 mm with such very tall (3m) species as Elephant Grass Pennisetum purpureum to 10-15 metric tons/ ha/yr in rainfall of 800 mm with such species as Hyparrhenia filipendula, Brachiaria brizantha, and Setaria sphacelata (vide e.g. Wrigley 1969). Whatever the species of grass left dominant in areas where grass fires are regular the total productivity of the grass layer per annum probably greatly exceeds that of the leaves and shrubs of the other vegetative layers in savanna. Again, whilst we have not been able to locate any precise figures, we believe this generalisation would be accepted by plant ecologists.

In grassland and woodland, the perennial grasses normally become dormant during long dry seasons, producing little green leaf. In response to fires, frequently caused by humans, a few green shoots usually emerge from the stool; but these probably weigh less than 1 % of the total amount of vegetative matter produced by the same grass stool later in response to rains. The starch reserves of grasses are stored below ground level in the dry season and, in tufted species, it is often possible to remove 90-95% of the total standing crop late in the dry season without impairing the subsequent vigour of the grass concerned. The material left standing at the end of a dry season contains very little moisture and burns very readily, resulting in fires which vary in temperature and effect according to the volume and moisture content of the available grass layer. Hot fires in tall dry grass kill shrubs down to the ground and suppress tree seedlings and suckers.

The trees are characteristically deciduous becoming more or less bare in the dry seasons. They retain enough moisture, however, to enable them to produce leaf and flowers at the end of the dry season before the grass (which may, or may not, have been burned)

springs again in response to rains. The outburst of new leaf at the end of a dry season and before rains is especially noticeable in the 'Miombo' or *Brachystegia* woodland, but occurs to some extent in any broad-leaved woodland. Some fire-resistant savanna trees (notably *Erythrina* spp.) flower before they produce leaf, though the production of both the abundant red *Erythrina* flowers, and of new leaf, normally precedes any heavy rain.

Thus, in normal broad-leaved savanna or woodland, vegetative production, except for some fruits, is at its lowest ebb towards the end of the dry season. Up to one month before the onset of heavy rain (or, occasionally, even earlier) savanna trees produce new green leaf and flowers, resulting in some available food supply for caterpillars and other insects. The grass layer, which may or may not have been burned, produces very little green material before the first heavy rains but responds immediately and with very vigorous production to the first heavy storms. Tufted grasses may be in seed-head within one month of the first heavy rain, though most flowering and seeding takes place late in, or at the end of, the rainy seasons. Trees which have flowered before the rains, fruit late in or just after the rains. Fruit of Ficus spp., for example, may be abundant late into the dry season.

(iii) ACACIA WOODLAND AND GRASS PLAINS: Very large tracts of East Africa, notably in regions D and C, but also elsewhere, are covered with mixtures of Acacia and perennial grasses, typified by the Acacia-Themeda savanna of, for example, Nairobi National Park, or the Serengeti Plains, near Seronera. Usually, broad-leaved woodland intergrades gradually with Acacia grassland; but sometimes the boundary between Acacia and Brachystegia is sharp; one can cross it in a few strides (Lamprey, pers. comm.) The tree canopy is normally reduced to well under 50%, often below 20% (Pratt, Greenway and Gwynne 1966); the trees are mainly Acacia spp., with pinnate leaves composed of very small leaflets, rapidly deciduous in the dry season. Broad-leaved trees occur mainly along riverine strips of vegetation and there are relatively few shrubs. Perennial grass, often Themeda triandra, Chloris, or Cynodon spp. becomes the most productive component of the vegetation, the amount of green material produced by the grass being enormously greater than that produced by the small leaves of *Acacia* trees. Again, no precise figures seem to be available (Pratt pers. comm.).

In such natural grasslands, all components of the vegetation-from the largest acacias to the leaves of stoloniferous grasses such as Cynodon dactylon-are consumed or affected by one or other species of large herbivore. Elephants Loxodonta africana and giraffes Giraffa camelopardalis can feed on, or kill, large trees. Grazing herbivores such as zebra Equus burchelli, buffalo Syncerus caffer, wildebeest Connochaetes taurinus and smaller gazelles such as Gazella granti and G. thomsonii utilise grass at all stages. Unlike forest, and to a greater extent than in most broad-leaved woodland, the nutrients in the ecosystem are thus constantly being circulated relatively rapidly by large browsing animals, grasseating species, carnivores preying on these, and finally decomposers. Although the grass dries off in the dry season, as in broad-leaved woodland, its bulk is seldom so great as in moist woodlands. It is frequently eaten down by large herds of herbivores, so that any fires are slow, creeping, and not so severely destructive of shrubs and trees. Grasseating herbivores form most of the biomass of large mammals utilising the environment.

If the large herbivores naturally occurring in this environment are eliminated (as they usually are-or have been, in the last fifty years), they are often replaced by large herds of domestic stock which utilise the vegetation in a much more selective manner and alter its composition. Tree species then tend to dominate or eliminate grasses. Suppression of fire and overgrazing by domestic stock results in dominance of tree species. The elimination of grass can sometimes result in dense Acacia thickets in areas quite recently dominated by perennial grasses. Apart from some areas in national parks and some areas outside national parks affected by tsetse fly Glossina spp., this process has already occurred over most of this vegetation type in most of East Africa inhabited by traditional pastoralists. The broad result is that more and more of the available nutrients in the ecosystem become locked up in standing timber, and the primary productivity of the grass layer is greatly reduced. Experiments have shown that clearing the woody species results in large increases in the productivity of grass (G. W. Ivens, Chapt. 18, Pratt & Gwynne 1977).

The cycle of annual events in this vegetation type resembles that in broad-leaved woodland. The trees retain moisture (to the tips of their twigs) throughout the dry season, producing new leaf and flower before any substantial amount of newly-growing grass appears. They leaf out and flower generally before the rains. Acacia species frequently produce very copious flowers, so that some nectar and its attendant insects are thus available for at least one month before heavy rains occur. At the end of the rains, many Acacia spp. produce an abundance of fruit, notably Acacia tortilis, which result in such quantities of pods that they carpet the ground beneath the trees and provide part of the diets of many large wild and domestic herbivores. Birds do not seem to eat them much at this stage, but the green pods of Acacia tortilis are eaten by White-bellied Go-away Birds and the seeds, infested by bruchid beetles, attract woodpeckers (C.-van Someren, pers. comm.).

In this type of country, grass does not produce much green leaf before rains have fallen though, after fire, a little green material may sprout from the base of perennial stools. Themeda triandra, often a dominant component of the grass layer in this type of country, flowers within one month of the first rains and continues to flower and produce seedheads over the next two to three months, until at least one month after the rains have stopped. The maximum bulk of grass herbage, possibly 10-20 metric tonnes/ha/rainy season (twice a year in Region D) is available about one month after the rains cease. Quantities of grass seed in head are also then available, thereafter gradually being reduced, but still available on the ground after the vegetative parts of the grasses have dried and are burned.

The amount of leaf and seed produced even by important tree species such as *Acacia tortilis* does not seem to have been recorded (Lamprey, Pratt, pers. comm.). In view of its importance as the main food supply of large wild or domestic herbivorous mammals, leaf and seed production in grass has been quite well studied, for example see Wrigley (1969). In this type of terrain also, most vegetation available in, and just after, the wet season is grass. During the

late dry season, more of the green vegetative material available may be in the form of tree buds, leaves, flowers and fruit.

(iv) THORNBUSH: In various forms, this is a characteristic East African vegetation type, covering vast tracts of Region D and smaller tracts of Regions A, C and E. Since it generally occurs in rainfall of less than 600 mm/yr and is typical of rainfall of 400-500 mm/yr, there is very little thornbush in Region B. Here, the situation characteristic of forest tends to be repeated on a lesser scale—that is, the majority of the available nutrients are tied up in standing trees and shrubs (in this case, usually less than 10 m tall) while the grass layer dominant in the vegetative productivity of woodlands and grass plains is much less important. Grasses present are typically annual or semi-perennial, notably Aristida, Brachiaria, Chloris, and Tetrapogon spp. They are characterised by comparatively small vegetative bulk, but relatively abundant seed production. As a result, probably, of reduced grass cover and therefore few fierce fires, the shrub layer is relatively abundant and dense, sometimes producing contiguous thickets up to 1.5 m high.

Most of the tree layer is composed of bushy species of Acacia such as A. mellifera, A. senegal, A. reficiens, A. mubica, with some taller A. tortilis especially along river valleys, and Commiphora spp. which, over vast tracts, form almost contiguous stands. There are a few larger trees such as Delonix elata, Melia volkensii, and the Boabab Adansonia digitata. Apart from a few unusual evergreens (such as Dobera glabra), almost all trees are leafless from shortly after the end of the brief rainy seasons to late in the dry season. Before the next rains, they come into copious flower, then new leaf.

In this vegetation type, the amount of green material produced by the trees and shrubs may often exceed that produced by grasses, although again there seem to be no precise quantitative data. In the rains, a dense canopy composed of the interlocking crowns of Acacia trees and shrubs shades out the grass below. Acacia thickets are often so dense that no substantial amount of grass can grow beneath them. Soon after the rains cease, the leaves of the acacias fall and carpet the ground, also producing quantities of pods. Broad-leaved Commiphora trees

(which are semi-succulent and unlike acacias) turn yellow and rapidly drop their leaves. The Baobab is naked in the dry season but produces green leaf in the rains.

The productivity of the ground layer of grasses and small herbs in this type of terrain is very variable, responding to the great variability in total annual rainfall, which is associated with reduction in mean annual rainfall. In a year of good rains, the annual and semi-perennial grasses grow vigorously and produce great quantities of seed. In poorly-drained soils, sedges Cyperus spp. may produce abundant underground tubers (Swank 1977). Much of the seed remains available throughout the subsequent dry season and, if the rains following are not heavy, much of it does not germinate but remains available to seed-eating birds. Large seed reserves on the ground are needed to enable annual grasses to take advantage of heavy erratic rains, reproducing abundant seed which lies dormant for several years.

In thornbush, there is a striking contrast between, on the one hand, brief periods of apparently lush growth and abundance of various food supplies (notably insects) in, and just after, relatively-brief rainy seasons; and, on the other, the apparent absence of anything green in the height of the dry season. Green material persisting through the dry season is often aromatic, poisonous, or latex-bearing-for example in the many arboreal Euphorbia spp. typical of the East African thornbush. However, since all birds inhabiting this type of country must survive through dry and wet seasons alike-and since they often become conspicuously abundant as soon as the rain falls-food supplies of various sorts permitting survival are probably more generally available than at first appears.

(v) SUBDESERT SCRUB AND DESERT: This type of vegetation covers over 200 000 km² in Region D and parts of Region A, but does not occur in the other three regions because the rainfall is too high. It occurs in annual rainfall of 200-400 mm, grades gradually into the lower-rainfall threshold of the thornbush vegetation type and is typified throughout by very low and erratic vegetative productivity.

Arboreal vegetation in this type of country is sparse. The few large trees are found mainly along

seasonal watercourses and in depressions, where—by reason of violent runoff in rare, but intense, storms over vast tracts of bare land—large amounts of water sometimes collect. Doum Palms *Hyphaene* spp. and some acacias, notably the adaptable *A. tortilis* are characteristic of such situations.

Most other woody vegetation consists of shrubs up to 1.5 m high, often succulent (for example, the Desert Rose Adenium somalense). Many perennial species have a relatively enormous spreading root system with comparatively little leaf growth above ground. Shrubby acacias are typically flat-topped, in the shape of a broad inverted cone, with a comparatively large upper surface, shading its own root system on the ground below. Such small trees or shrubs manage to survive through protracted and very hot dry seasons, perhaps not flowering and seeding every year.

The ground layer of herbs and grasses is largely annual or succulent, with semi-perennials and perennials in depressions, or along water courses, dependent on seasonal runoff. Short-lived annuals typically have a small root system, short and weak upper parts, and produce a great abundance of flowers and seeds. Seed remains available in the ground surface for years, and germinates to reproduce itself again whenever adequate rain falls.

Thus, this type of terrain is characterised by an overall scarcity of vegetative material with the possible exception of abundant seed, very little persistent insect life dependent on green material and an extreme alternation between protracted periods of privation and occasional periods of extraordinary abundance. Heavy rain can transform an apparently lifeless expanse of volcanic dust and boulders into a marsh swarming with amphibia and surrounded by tall grass and herbs alive with grasshoppers and other insects (Dida Galgala, northern Kenya: December 1963, L.H.B. pers. obs.).

This very brief, and necessarily over-simplified, account of the extremely complicated and varied ecology of our region helps to explain why breeding seasons of birds can vary from opportunistic—taking advantage of brief good rains in semi-desert—to perennial, in more equable conditions. However, it will be clear that, in some areas, the breeding

seasons of birds—relatively restricted as they are—are not necessarily directly proportionate to the primary productivity of any vegetation type. It is not surprising to find opportunistic, short-term breeding in subdesert, but much more surprising to find relatively short and well-defined breeding seasons in a forest environment where at least some vegetative productivity is available year-round.

- (b) Seasonal Availability of Specific Foods: The available foods for birds can again be divided into vegetable foods, such as buds, leaves, flowers, nectar, fruit and seeds; or animal foods—themselves dependent on vegetative production—such as insects and other invertebrates, amphibia, fish, reptiles, birds and mammals. Each of these possible sources of food will be discussed briefly in relation to seasonal abundance, so far as it is known.
- (i) BUDS AND LEAVES: Buds are eaten by several species of birds, notably mousebirds Coliidae and some vegetarians of arid country such as the White-bellied Go-away Bird which feeds much on Acacia buds and leaflets. Buds and young leaves are most abundant late in the dry season and in the early rains. General observations suggest that they are more important as a means of keeping alive in dry periods than as a main food supply during breeding seasons. For instance, the depredations of the Speckled Mousebird on leafy vegetables near Nairobi are likely to be much worse in a dry year than in a wet, when more natural food may be available. Mature, fully-expanded leaves, available later in the rains, are probably unimportant as a food supply for any bird species, except possibly the Ostrich.

No bird species appears to be entirely dependent on the leaves of grass, though some geese regularly graze waterside grass. However, leaf-blades of perennial savanna grasses are frequently important as nesting material. For example, the Red-billed Quelea cannot breed until adequate rains have provided enough building material necessary for huge colonies of millions of nests. This would similarly affect many ploceid weavers, though some use other building materials of perennial nature. Since some suitable material is available within a few weeks of the onset of rains, lack of building material is probably not an important limiting factor for most

ploceid weaver birds which have negligible effect on the total bulk of green grass blades available.

(ii) FLOWERS AND NECTAR: Flower buds and petals are eaten by mousebirds and some other species. However, they do not appear to be important staple foodstuffs for any species and, like buds and leaves, are probably more important for survival than as a food supply necessary for breeding.

Nectar is likely to be most important for sunbirds Nectariniidae, though possibly a few other species feed on it, to some extent. In East Africa, there does not seem to be any local counterpart for the abundant nectar produced by, for example, *Bombax* species and the Dhak tree *Butea monosperma*, typical of Indian woodlands and forests, and which is consumed by a wide variety of birds, from small sunbirds to parrots and crows (L.H.B. pers. obs).

The supply of nectar in many urban areas, notably in and near Nairobi, has been greatly affected in the last half-century by increased planting of nectarbearing exotics, such as *Bignonia*, *Fuchsia* and *Salvia* spp. Since many breeding records of sunbirds come from gardens, breeding seasons may have been locally affected by such planting.

Sugars are the main solutes present in nectar, with only traces of protein, mainly as enzymes. Nectar-feeding sunbirds must therefore supplement this food with protein, both for adult maintenance (including the needs of the female for egg production) and growth of young. The most likely source of this is insects attracted to the nectar. Availability of nectar itself may not therefore be a crucial stimulus to breeding. Rather, flowers provide both nectar and pollen (whose exploitation by birds does not seem to have been positively recorded) and attract insects as a source of protein (Reynolds, pers. comm.).

The seasonal importance of nectar for several sunbird species (in an area of northern Nigeria climatically like our Region A) has recently been discussed by Pettet (1977), especially in connection with the Scarlet-chested Sunbird and the Pygmy Sunbird. Both occur in East Africa, the Scarlet-chested Sunbird being common and widespread. Pettet found that Scarlet-chested Sunbirds fed extensively on the nectar of ornithophilous tree species during the dry season, but were not in

breeding condition at this time. The Pygmy Sunbird is a dry season breeding visitor to northern Nigeria, feeding extensively on the nectar produced by dryseason flowering Acacia spp. (A. albida, A. seyal and A. nilotica) and of Butyrospermum, but absent when some of the commonest Acacia spp. are in flower.

In East Africa, Erythrina, Acacia, and Albizzia spp. flower mainly just before the rains, twice a year, in markedly bimodal rainfall regimes such as most of Region D. Loranthus spp. can flower both in wet and dry seasons, as can various species of aloes. Leonotis spp., much sought by many sunbirds, flower in and after rains. There is thus a supply of nectar from various flowering plants for much of the year, but it may reach a peak in the late dry season when Acacia and Erythrina spp. burst into flower together over thousands of km².

Although the breeding seasons of sunbirds are often quite widespread, analysis of the available records shows that most species breed mainly in the rains, sometimes in the early rains, suggesting that supplies of nectar (or perhaps associated insects) could be important to initiate breeding. However, for most species where the records are adequate (10 or more for any climatic region), it seems that nectar itself is not critically important for breeding. In sunbirds, as in many insect-eaters, there is often a long rains peak in Regions B and D with bimodal rainfall, suggesting that insects are more important for breeding purposes than supplies of nectar. Montane sunbirds breed most in the dry seasons, but this may be for climatic reasons rather than because of available food supply.

(iii) FRUIT: Some fruit is available year-round. However, in most of the more abundant fruiting species (in genera such as Ficus, Trema, Cordia, Maesopsis), most is available in the dry season. Again, the planting of exotics such as Cotoneaster rould result in a source of bias for some species.

Some fruit-eating species (fruit pigeons, hornbills, turacos, parrots, barbets, starlings for example), are highly mobile and can congregate in numbers in fruiting trees, while others (notably skulking forest greenbuls) are not so able to reach such temporarily abundant supplies, unless they happen to occur in

their territory, and must subsist on smaller supplies of fruit available in the undergrowth.

As fruit is mainly available in the dry season, one would expect most fruit-eating birds to breed in dry seasons. Many species (notably starlings and barbets) do so, but exceptions to this general rule include mousebirds, which tend to breed most often during and late in the rains but are less exclusively dependent on fruit, however, than are some other fruit-eating species.

(iv) SEEDS: Seed supplies are chiefly of two kinds, abundant grass seed produced in grasslands and woodlands, and seeds of flowering herbs, especially of Compositae. Seeds contained within fruit-for instance, of Trema, Physalis, Nicandra spp. (C.-van Someren, pers. comm.)—can also be important. In L.H.B.'s garden there is a large Croton macrostachyus tree which is in fruit June-July and December-January, at the end of each rainy season. When the fruit of this tree is being eaten by bulbuls, mousebirds, small barbets, and orioles, the seeds are mainly discarded and fall to the ground, where they are eaten by numbers of doves Streptopelia, Aplopelia and Turtur spp. These are thus partially dependent on the fruit-eating activities of the other birds in the tree above and would otherwise have to wait till later when maturation and drying of the fruit would release the seed naturally. Ward (1971) showed that seed supplies on and near the ground reach maximum availability early in the dry season, the supply thereafter diminishing gradually until, just before the rains, it is low. With the onset of the rains (whatever the rainfall regime considered), supplies of seeds are further reduced through germination. In grass (and flower heads), seed supplies again become abundant towards the end of the rainy seasons and fall to the ground as the grass dries off. Annual or seasonal fires do not seriously affect the supply of seed and, by removing dense dry vegetative cover which could impede searching, may make it more easily available to searching birds.

The maximum abundance of all kinds of seed whether from grass (often the most abundant supply), seed heads of flowering herbs or from dried tree fruits, occurs late in the rains and through the first half of the dry season. Birds more exclusively dependent upon seed supplies could therefore be

expected to breed most often later in the rains or early in the dry season, and this is very often the case. However, the extent to which seed-eating birds feed their young on softer material, including insects, is often imperfectly known. Moreover, Swank (1977) showed that some supposed seed-eaters (Crested Francolin) depend to a surprising degree on insects, while many larks, which breed mainly in the wet season, lay when the seed supply is least and feed their young mainly on insects (Reynolds pers. comm.) Often, however, there is good correlation between maximum supplies of seed and maximum breeding by seed-eating birds.

(v) INSECTS AND OTHER ARTHROPODS: Generally speaking, insects become more abundant during the rains and reduce in numbers, or become scarce during the dry seasons. In areas with bimodal rainfall peaks, with most rain April-May and November-December, there are two peaks of insect abundance during the year. Although this statement is made largely on general evidence and opinion, it is supported by a short but useful paper by Dingle & Khamala (1972) giving some quantitative data on the relative abundance of insects in an area of Acacia-Themeda grassland near Nairobi National Park from October 1969-July 1970. Their data are hard to interpret in terms of biomass per unit area, but are based upon 1000 sweeps of a net 40 cm in diameter. They also neglect lepidopterous larvae, which are certainly an important source of food for some species of birds. However, they show that the biomass of insects in May, late in the long rains, was more than four times that in January, towards the end of the dry season, while the number of individuals and species represented were both nearly doubled. They also found that insects increased in the short rains, November, although the result was somewhat obscured by the fact that, in October, about half the total biomass was composed of two large grasshopper species. Although this result is based upon only six counts over a period of less than a year, and although it ignored some insect food important for many species of birds, it basically confirms what would be forecast from crude general observations-that insects increase in abundance with the onset of rains. There is a marked increase in abundance in the long rains in Region D and

a lesser but still noticeable peak in the short rains. Our records indicate, however, that most insectivorous birds in Region D take advantage of the greater long rains peak, but not proportionately of the smaller short rains peak of insect abundance, though some species do show a second breeding peak in the short rains.

These authors also quote Owen (1969) to the effect that, in Kampala (Region B), there was a marked increase in insect abundance in the long rains April-May, but relatively little change in abundance in the period September-December. Reference to the rainfall histogram for Kampala (Fig. 1) shows that the secondary peak of rainfall at this season is more prolonged but less abrupt than in April and May. As this paper was going to press, A.R.E. Sinclair published observations on insect abundance and breeding seasons in the Serengeti, our Region C (Sinclair 1978). This paper is based upon the records with which he provided us, combined with some other records derived from Betts (1966) also available to us, totalling 301 records -considerably less than the total material available to us from the same region. Breeding seasons of insectivorous birds are correlated with an index of insect abundance, based upon collections from light traps over three years and some sweep samples. The author also advances the theory that the rapid increase of insect life which, within 24 hours, follows the onset of rains is due not only to the emergence of aestivating adults, or the hatching pupae within the area, but also to the arrival of migrants, wind-borne on the rain fronts of the inter-tropical convergence zone. Further, Sinclair suggests that the timing of the breeding peak, in ground-nesting insect-eaters and others, is directly related to their size-small larks breeding first, then plovers (Vanellus spp.), then smaller and larger bustards, finishing with the Ostrich, the largest, in the following dry season. This somewhat novel concept is not supported in some groups by our own more detailed records, which show, for instance, that in plovers of the genus Vanellus, a breeding peak occurs during rains in drier areas of their range and in the dry season in wetter areas. Sinclair also admits that the Ostrich is omnivorous rather than purely insectivorous, and points out that hatching in September (which he suggests might be due to the long period

required for a female Ostrich to build up reserves sufficient to lay a clutch of eggs) may be disadvantageous to the survival of the young, as it occurs at a time of decreasing food availability.

All these papers underline the need for more careful and precise observations to correlate insect abundance with the breeding seasons of insectivorous birds. Basically, they show that the general observation that insects increase with the onset of rains is correct; and Owen (1969), in showing that there is a more marked increase of insects in the long rains April-May than in the short rains September-December, helps to explain why, in Region B, there is a clear breeding peak among forest insecteaters in this region during the long rains. None of these papers explains, however, why there is not a proportionate increase in breeding among insectivorous birds in the short rains, when there is apparently a lesser but still marked peak in insect abundance; nor do they explain why there should be a marked peak in breeding by birds in the short rains in northeastern Tanzania (Moreau 1950, Beesley 1973), when this period might be expected to coincide with a smaller peak in insect abundance. Evidently, although there is a considerable biomass of insects available year-round, breeding among insectivorous birds is not directly proportionate to insect food supply. Although such a result may not be considered inevitable, it is also clear that while many insectivorous birds do not breed in direct proportion to the availability of insect food, some others, which (notably in Region D) show roughly proportionate breeding peaks in both long and short rains, do so to take advantage of an available food supply.

The actual supply of insect food should also be related to the foraging strategies of insectivorous birds. The abundance of insects early in the rains may be due to migration (as Sinclair (1978) suggests); emergence from aestivation of imagines which have been hiding in crevices in bark, etc; emergence of alate termite and ant swarms; or the hatching of imagines from pupae which have lain dormant through the dry season. For such birds as woodpeckers, with their specialised foraging techniques, such 'dormant' supplies may be as (or more) important than flying insects and may actually be more abundant in the dry season. Betts (1952) associated

breeding seasons of woodpeckers in southern India (in climates not very different from much of East Africa) with maximum development of wood-boring larvae and their approach to the surface prior to pupation and emergence as imagines with the first showers in March. Our records for such 'searching' insect-eaters as woodhoopoes, woodpeckers, and crombecs show that their breeding seasons are more extended than for typical forest insect-eaters feeding principally on flying insects or those which fall abundantly to the ground from trees, or available because attracted to flowers, or larvae feeding on green leaves. The total availability of insect food is not the only factor to be considered in relation to the timing of the breeding season. It is, however, extremely striking that the total supply of insectswhich, at least in Region D, is bimodal—is not correspondingly reflected in two proportionate peaks in the majority of insectivorous birds occurring there.

Termites are a special case. Their alate (flying) swarms occur after heavy storms in the rains and the abundant food so provided is consumed by a very large variety of birds that usually feed on other supplies. Termites are eaten not only by small insect-eaters such as swallows and flycatchers but by normally fruit-eating starlings, hornbills, several small raptors (the Hobby Falco subbuteo and African Hobby F. cuvieri and even large eagles and vultures). When not swarming during the dry season, they are nevertheless quite abundant on the ground surface; in semi-arid regions, they may play a crucial part in keeping birds alive when other food supplies are short. Further study of the importance of termites is desirable.

Other terrestrial arthropods are probably much less important as food supplies for birds than are insects. Little is known of their cycles of abundance; but millipedes, which become most abundant in the wet season, are not much eaten by birds. Others (such as scorpions and solifugids) hide by day under stones and logs and are not therefore vulnerable to any but rather powerful birds—possibly Ground Hornbills—which can overturn such objects. They may emerge by night, but since they are flightless, are unimportant to nocturnal aerial hunters such as nightjars, though solifugids and scorpions are eaten by some owls (C.-van Someren, pers. comm.).

(vi) OTHER INVERTEBRATES: These include worms, small crustacea, molluscs and other organisms frequently found in mud along lake shores and elsewhere. Little is apparenty known of their cycles of abundance or of their importance as food for certain bird species, though the breeding cycle of the Open-billed Stork has been correlated with the emergence from aestivation of Pila snails (Kahl 1968). They are perhaps most likely to be important (together with larvae of insects such as chironomids) to aquatic non-passerines, such as the smaller plovers, Avocets, some ibises, and even Greater Flamingos (which feed largely on chironomid larvae and small crustacea (Ridley, Percy & Moss 1955)). Molluscs may also be important in woodlands and wet forests (C.-van Someren, pers. comm.) and Sessions (1972) found crab remains commonly in pellets of the Cape (Mackinder's) Eagle Owl.

In aquatic environments, such food supplies are likely to be perennially quite abundant, though we know of no published quantitative measurements of such organisms. Observations along a tropical lake shore give no impression of frenzied and constant searching for scarce food by plovers, rails or ducks. If food supply were the sole governing factor controlling breeding seasons, some birds would probably breed in all months. However, available records for most of the better-known species, show rather definite peaks usually occurring during the cool, mid-year dry season in Region D (whence most of the records come), with some apparently inexplicable variations, such as Kittlitz's Sandplover in Region C. Also, too little is known about the specific food preferences of many of the birds likely to subsist, mainly or wholly, on other invertebrates. However, the rather well defined breeding peaks shown by many aquatic and shore birds in areas where there should be plenty of food for much of the year suggest that, where food is perennially abundant, climatic factors may determine the breeding seasons.

(vii) AMPHIBIA: The cycles of abundance of amphibia are clear-cut. They can only breed in wet situations, so that they are everywhere most abundant in and after the rains, with bimodal peaks in Regions B and D. In arid areas they are not available at all in dry seasons, but temporary ponds are soon alive with amphibia after heavy rains. Most frogs have

an enormous breeding potential, but are highly susceptible to predation, and adverse weather, so that populations may fluctuate, from year to year, by factors of hundreds or more. Even in perennially aquatic habitats, breeding occurs most in the rains, though the breeding of the Clawed Frog *Xenopus* is not triggered by rain and its tadpoles are likely to be available throughout the year in permanent water (A. Duff Mackay, pers. comm.).

Few birds are known to depend primarily on amphibia and, by probing techniques, some that eat many-for example, the Yellow-billed Stork-can locate them in bottom mud. They are probably important to the Little Grebe and the Hamerkop and are taken as supplementary food supply by many herons, storks, ibises and spoonbills, and by some raptors, notably African Marsh Harriers and the Banded Snake Eagle. The Little Rush Warbler has been seen feeding nestlings on sedge frogs Hyrerolius (Reynolds, pers. comm.). Amphibia may play a part in the timing of breeding seasons of herons and egrets, which are so conspicuously triggered by the onset of heavy rain. However, good quantitative studies of their importance to such birds are lacking, and it is unlikely that the unreliable supply of amphibia actually controls the breeding season of any bird species.

(viii) FISH: These are the staple food of many large water birds, some of which—cormorants and grebes, for example—hunt them by diving and catching them below surface; others by swimming and catching them near the surface (pelicans); and yet others—storks and herons—whilst wading in shallow water, by stalking and stabbing them. A few—such as the Osprey and Fish Eagle, some gulls and terns, and kingfishers—catch them by aerial attacks from perches, or by hovering. The different strategies employed by fish-eating birds may well be as important as the abundance of certain fish, while other factors such as the opacity of the water must be important to fish-eating species that hunt by sight.

Seasonal effects upon certain species of fish not otherwise easily caught may render them very vulnerable to attack. Many—Barbus, Labeo, Clarias, Alestes, Haplochromis spp.—undertake spawning migrations upstream from Lake Victoria and, at such times, congregate near the mouths of inflowing

rivers, or below obstacles such as water-falls, dams and fish traps, where they are easily taken. Some species (such as lungfish and bichirs Protopterus and Polypterus) aestivate in drying mud in the dry season and emerge in the rains. Some catfish (Clarias) are nocturnal and so normally escape herons and other birds, but, in rains, swarm upstream and then become very obvious and vulnerable. Flooding of swampy areas by seasonal rivers also results in pools in which fish are trapped after the waters recede and are easily caught by many fish-eating birds (see e.g. Kahl 1966). Most fish are likely to be most easily caught in, and alongside, rivers and swamps during and just after the rains, though opacity of the water in floods must reduce their availability to birds that hunt by sight.

In alkaline lakes, the biology of the small Tilapia grahami has been fully studied by Coe (1966). Since its introduction into Lake Nakuru in 1960-61, this fish has become the staple food supply of a huge population of fish-eating birds, and similar alkalitolerant species occur in Lakes Natron and Manyara. The fish breed at most times of the year, but when populations are high they become subject to mass mortality, resulting in a tide-line of dead fish. Coe suggests that such an occurrence is due to gillclogging and anoxia. This pattern of a small population of one or more specialised fishes building up to enormous numbers and thereafter crashing with suddenness, seems typical of alkaline lakes but inortality has not occurred so dramatically at Lake Nakuru—perhaps because of the huge quantities (certainly over 3000 metric tons/yr) already harvested by fish-eating birds. Abundance and die-off has been observed at Lakes Magadi and Natron in the rains (Coe 1966) and at Lake Natron in the mid-year dry season (Brown & Urban 1969). The latter die-off was believed to have suddenly halted breeding in a huge colony of Great White Pelicans.

In more stable freshwater lakes, fish populations are likely to fluctuate much less. At Lake Naivasha, introduced *Tilapia* spp. and Large-mouthed Black Bass *Micropterus salmoides* are abundant in shallows year-round. If breeding of large water birds depended on the actual availability of these fishes as food supply, some should breed in every year, and for most of the year. However, the situation seems to be that, apart from cormorants, the African Darter and the Goliath

Heron, which have fairly widespread breeding seasons, other large fish-eating herons and storks do not breed every year; and, when they do nest, they breed prolifically, normally during rains. In these cases, it is difficult to reconcile perennially available fish supplies with either season or the numbers of fish-eating birds breeding.

(ix) REPTILES: A few raptors—such as the snake eagles (Circaetus), chanting goshawks (Melierax), the Shikra and Pygmy Falcon, prey principally on reptiles, which may also be important in the diet of such species as rollers (Coracias) and ground hornbills (Bucorvus).

Reptiles, being poikilothermous, are not numerous in cold climates above 2000 m A.S.L. but are relatively abundant in hot dry localities.

Little seems to be known about the population of snakes and lizards in the environments concerned. Many snakes are nocturnal, and are therefore unavailable to diurnal predators, and the activity of lizards is largely controlled by ambient temperature. Snakes and lizards are often cryptically coloured. In desert situations, reptiles may become an important source of food for large raptors that elsewhere would prefer other foods, such as gamebirds. Western (1974) summarised data from a semi-arid locality in Turkana (our Region D) for 13 species of lizards, and found populations of from 5.3-690/ha, and biomass of 0.19-2.49 kg/ha. Peak activity was from 08.00-11.00 hrs and again from 15.00-18.00 hrs, avoiding the night and the hottest part of the day, He also cites Duff Mackay (1965) who, in Turkana, collected 7000 Saw-scaled Vipers Echis carinatus in 600 km² in three months without apparently reducing the population. Western (1974) considered that, in his study area, the biomass of snakes might exceed that of lizards, and that the total biomass of snakes and lizards might be of the order of 2-3 kg/ha—about 10-15% of the mean biomass of large mammals. Although these figures are valuable as an indication of a surprisingly large reptile biomass, they do not indicate any seasonal variations. However, since activity of reptiles is largely governed by ambient temperatures, it might be reasonable to suggest that they are most likely to be active and available in warm conditions and low cover late into the dry seasons. This would coincide with laying in the late dry season in chanting goshawks *Melierax* spp. but other reptile-eating raptors (snake eagles, Bateleur) may have more widespread breeding seasons. In warm climates, reptiles are probably available in some numbers year-round, but may move about more freely by day during wet seasons (C.-van Someren, pers. comm.).

(x) BIRDS: These are important as food for certain raptors, including Accipiter spp., Ayres' Hawk Eagle and some falcons (which prey mainly on small birds or doves) and larger eagles, which prey mainly on gamebirds. Small birds, either in forest or woodlands, are most likely to be abundant (according to the breeding data in this paper) after rains and, especially, in forests and some woodlands and grasslands, after the main rains in areas with bimodal rainfall peaks (Regions B and D). Generally speaking, accipiters and falcons breed in the mid-year dry season in such areas, so that correlation between maximum food demand and seasonal abundance of prey is at least fairly good. Where records are adequate, they suggest that gamebirds tend to breed in and just after both rains, so they are most numerous, and young perhaps easiest to catch, in both dry seasons, or the main dry season in monomodal rainfall regimes. Raptors dependent on these species breed most often in dry seasons and, in areas with bimodal rainfall peaks, prefer the cool mid-year dry season in Region D, but probably the hot dry season October-February in Region B.

(xi) MAMMALS: Small mammals—notably rodents, such as the mole rat Tachyoryctes, and the grass rats Arvicanthis and Mastomys—are important, if not staple foods of some raptors, notably Elanus, Buteo spp., Tawny Eagle, some Falco spp. and several large owls. The hedgehog Atelerix seems important to Verreaux's Eagle Owl and mole rats are the staple of the Cape Eagle Owl.

Cycles of rodent abundance have been mainly studied in relation to crop pest situations. Rodents normally increase during the rainy seasons, sometimes reaching a peak of abundance well beyond the capacity of any socially-regulated raptor population to limit it. Low populations in tall grass may be extremely hard to see and locate, but in more arid localities even small numbers are quite obvious and may be

easily caught. Most of the rodent-eating raptors breed in or after the rains—especially, in Region D, during the long rains and mid-year dry season. These times of breeding may coincide with peaks of rodent abundance, but are also coincident with peaks of vegetative cover.

Medium sized mammals such as hyrax (Hyracoidea) and hares (Lagomorpha) are important only to a few large eagles. Although hyrax breed at any time of the year (Sale, pers. comm.), Verreaux's Eagle breeds in the dry season in monomodal rainfall regimes and in the mid-year dry season in Region D, with bimodal rainfall. This suggests that climatic considerations are more important to Verreaux's Eagle than the actual availability of hyrax.

Larger mammals are important to eagles. The small Suni Antelope Nesotragus moschatus, which is the staple diet of the Crowned Eagle, has not been studied in detail but probably breeds in both rainy seasons, as do dikdik Rhynchotragus spp. In Tsavo National Park dikdik are very important prey items for four large eagles (Smeenk 1975). They are the Tawny and Bateleur Eagles (normally more dependent on small mammals and snakes) and the African Hawk Eagle and Martial Eagle (which feed primarily on game birds). Tsavo records for all these species (except the Bateleur, which has a more elastic season) indicate peak breeding in the mid-year, cool dry season, though dikdik can also produce young in the more-reliable short rains. This again suggests that climatic factors are more important and that any correlation with an abundant food supply is coincidental. The Crowned Eagle lays most often July-October in Region D, with young in the nest and maximum food demand October-December. There is no evidence that this is connected with abundance of food supply, while dense cover conditions would then obstruct easy capture of prey. Also, since individual female Crowned Eagles can vary their laying dates by as much as six months, according to circumstances (Brown 1966), it appears unlikely that food supply is important in controlling laying dates and breeding seasons in this eagle.

Very large mammals are important only when dead to carrion feeders, the Marabou Stork and vultures. Where these have been studied in sufficient detail in the Serengeti (Houston 1976, Pennycuick 1976), data suggest that, in Rüppell's Griffon and

White-backed Vultures, breeding occurs at times enabling recently-fledged young to compete effectively with adults for abundant carrion. However, evidently the same factors do not affect the Lappet-faced Vulture, which produces fledged young in the rains, when carrion is not plentiful.

Carrion is everywhere most abundant at the end of a severe dry season and early in the subsequent rains, but the supply varies enormously from year to year. In some years, catastrophic losses among domestic stock (of the order of 60% of the total) produce far more carrion than all the available mammalian and avian scavengers can cope with, while in other years they may go short. So far, there are no quantitative studies of breeding success to suggest that large scavenging birds breed less often, or less successfully, in years when carrion is less abundant. In the case of the Marabou Stork, the only thorough study (Kahl 1966) was done in an area where artificial food supplies from the western Kenya Kitale butchery obscured such factors.

5. Analysis by groups of species

In this discussion of various possible factors and their effect on particular species or groups, it is convenient to start with the groupings proposed by Moreau (1950) which have been followed by several other authors on this subject (e.g. Beesley 1973, Benson 1963). Based on these original groupings, our much more detailed data permit further subdivision. In some groups (notably the large raptors), still more detailed data invites further discussion

Moreau 1950

- (1) Evergreen forest birds
- (2) Water and swamp birds
- (3) Raptors (hawks, eagles, vultures, owls)
- (4) Ground birds (plovers, gamebirds, nightjars etc.)
- (5) Grass birds
- (6) Others, predominantly passerine, insect and fruit eaters
- (7) Seabirds

(in text under individual species and, where relevant, recapitulated here) of more specific factors affecting the timing of breeding scasons.

Moreau's original grouping and our additional subdivisions are as follows:

Moreau's six basic classes of land birds (which he himself would have subdivided if adequate data had been available) can thus be further divided into at least 12 groups, based largely on different preferred food supplies. Where data are adequate, each can be further discussed in relation to nesting sites, ecology of the habitat, and other factors. Within some large groupings—for instance, among raptors—further subdivision is possible according to preferred food supplies. Some of these can be covered in detail, since not only is their basic food known, but the behaviour of both sexes in relation to the feeding of the young has also been observed in detail.

However, while indicating that many species require individual treatment and in relation to other factors (such as length of breeding cycles), in most cases sufficiently detailed data do not exist. For instance, among forest insect-eaters, it would be pointless at this stage to subdivide the group into feeders in the canopy, undergrowth, mid-level or on the ground—although for some individual species we have discussed such possibilities when sufficient data exist.

We have already discussed the breeding of most seabirds in East Africa (Britton & Brown 1974). Moreau covered a much wider field in his review of seabirds, and since then much new work has been done on Ascension Island (e.g. Ashmole 1963)

This study

- (1) Forest insect-eaters
- (2) Forest fruit-eaters
- (3) Fish-eating water birds
- (4) Other water birds, vegetarian or feeding on invertebrates
- (5) Raptors, further subdivided into insect-eaters, fish, reptile, bird or mammal eaters, when adequate data exist.
- (6) Ground-dwelling seed-eaters
- (7) Other ground birds (plovers, nightjars etc.)
- (8) Grass-dwelling secd-eaters
- (9) Insect-eaters living in grass
- (10) Miscellaneous seed-eaters
- (11) Miscellaneous fruit-eaters
- (12) Miscellaneous, all others
- (13) Seabirds (mainly Laridae)

and on islands in the Indian Ocean (e.g. Diamond 1975). The coastal environment in East Africa affects mainly some of the Laridae (the rest breeding on inland lakes and rivers); it also affects herons and egrets and a few other species including the White-fronted Sandplover and Fish Eagle. Our data suggest, in the case of Laridae, that climatic factors rendering islands close to shore less accessible to raids by local fishermen, may be more important than the availability of food supply in determining breeding seasons.

Group (1) Forest insect-eaters: Among non-passerines these include forest guineafowls (which feed partly on insects) some cuckoos and coucals, nightjars and swifts, both trogons, some kingfishers, bee-eaters and rollers, some wood hoopoes, the smaller hornbills (Tockus) at least in part, and some wood-peckers. Many of these are hole-breeders or ground feeders and rather few (e.g. trogons) really resemble forest insectivorous passerines.

Most forest passerine species are insectivorous, either entirely or partly, when feeding young. They include all broadbills and pittas, helmet shrikes and shrikes (the latter also partly carnivorous); drongos, orioles (which also feed on fruit) and cuckoo shrikes, many bulbuls and greenbuls, many turdids, all warblers and flycatchers, some sunbirds (which also feed on nectar), white-eyes and some ploceids and estrildids. Some seed-eating *Serinus* spp. may also feed their young on insects, though as adults they subsist mainly on seeds. Bulbuls and greenbuls, turdids, white-eyes, ploceids and estrildids take fruit as adults.

The breeding seasons of forest guineafowl and francolins tend to be more prolonged and ill-defined than those of their savanna or semi-arid country relatives but data are often very scanty. The forest dwelling Emerald Cuckoo breeds in the long rains in Region D, a time tied to that of its hosts. The Yellowbill and Blue-headed Coucal (the latter perhaps not a true forest bird) breed in the dry season, and in both dry and wet seasons respectively, according to rather scanty evidence. The Mottle-throated Spinetail, is reported (twice) to breed in the dry season. Trogons, one of the few non-passerine groups habitually feeding on insects

above undergrowth and below the canopy level, breed mainly in the long rains (in rather marginal habitat) in Region D. Forest kingfishers breed in both wet and dry months, the Pygmy Kingfisher possibly preferring the end of the rains. Very scanty evidence suggests that true forest bee-eaters breed at the end of the dry season. The forest rollers Eurystomus clearly prefer the rains, but the rather scanty evidence for the White-headed Wood Hoopoe indicates widespread breeding, with some preference for dry months. The forest Tockus hornbills (though there are no records for those species truly adapted to forest, such as the Red-billed Dwarf Hornbill) breed in both wet and dry months, seemingly preferring dry periods. The few available records for forest woodpeckers are about equally divided between wet and dry months.

Thus, among non-passerine forest insect-eaters the frequently expressed view that, in this equable environment, breeding may occur at any season, is generally supported. Exceptions are in cuckoos, which are tied to the breeding seasons of their normally insectivorous hosts; trogons which depend more closely upon insects caught within the canopy than do most other non-passerines, and which clearly prefer rains breeding, and forest rollers which also clearly prefer rainy seasons. Although the data are generally too inadequate to permit very sound conclusions, it often appears that non-passerine forest insect-eaters are adaptable and can breed at many times of the year.

Among insectivorous forest passerines, this is not so. Most species show a marked preference for the main rains, though those species (or individuals) which breed in relatively-cold montane forests usually prefer the dry season. Forest-loving greenbuls and bulbuls tend to have widespread breeding seasons, but with a marked peak in the main rains. Here, the scanty records for many species generally support those for the relatively few, better documented species. Montane greenbuls, however, clearly avoid the heaviest rains. Among turdids, there are some curious exceptions to otherwise general trends. For instance, in Region E, the Eastern Bearded Scrub Robin definitely prefers the dry season, both in song period and in nesting records. The Abyssinian Ground Thrush, although montane, is nevertheless recorded breeding only in the early rains. Among many genera of warblers and flycatchers, there is some breeding in the dry season, or ill-defined breeding seasons but, although montane species may avoid cold, wet weather, a preference for breeding in the main rains seems frequent.

Breeding in these species does not appear to be directly proportionate to rainfall and the food supply that might be expected to accompany it. For instance, in the Red-bellied Paradise Flycatcher, 35/45 records are April-June, peaking in April; in the White-eyed Slaty Flycatcher—not a true forest species—the long rains April-June are preferred in most of Region D, but the short rains near Arusha, October-January. Most forest weavers, mostly or wholly insectivorous, breed mainly in the rains as—for preference—do some species that are seed-eaters, such as the Thick-billed Seedcracker. They tend to show a similar (but perhaps less defined) pattern to that of their relatives outside forests.

Group (2) Forest Fruit-eaters: Among non-passerines, these include several pigeons, forest parrots, some turacos (Tauraco and Corythaeola), large hornbills of the genus Bycanistes, and all forest barbets. Forest honeyguides, such as Cassin's Honeybird which may parasitise barbets, white-eyes, or sunbirds, are tied to the breeding seasons of their hosts. Among passerines, most of the true fruit-eaters are starlings e.g. in the genera Onychognathus, Poeoptera, Lamprotornis and Cinnyricinclus. However, some greenbuls also eat berries and fruit, though they may feed on insects too, perhaps especially when rearing young (van Someren 1956). Rather few have been studied in any detail and many are birds of the undergrowth, where fruit is not easy to find. A few seed-eaters Serinus spp. may also eat fruit, but they are probably more interested in the seeds within the fruit than the fruit pulp, which may be discarded.

The Olive Pigeon, Bronze-naped Pigeon and Green Pigeon breed in both wet and dry months, with an apparent preference for dry seasons in the Olive Pigeon. The Green Pigeon (not exclusively a forest bird) has widespread breeding in all regions, but probably a peak in and after the short rains in Region D (19/27 records November-February). The very scanty records for the Red-fronted and the Grey Parrots refer to the dry season, the short rains

(Red-fronted Parrot), or the mid-year break in the main rains (Grey Parrot, Region B). Most of the turacos are poorly documented, with one or a few records only, but these indicate both dry and wet season breeding. The better documented Hartlaub's Turaco and the Great Blue Turaco both breed in many months, but in Hartlaub's Turaco most records are for the mid-year dry season in Region D and in the Great Blue Turaco for the main dry season October-February. Hartlaub's Turaco records may be affected by artificial food supplies in Nairobi gardens, from where most of the records come. Turacos build very flimsy nests, which could collapse in violent storms of wind and rain. Forest hornbills of the genus Bycanistes, for which there are generally few records except for the Black & White Casqued Hornbill (Kilham 1956), prefer the main dry season in Region B; but the Silvery-cheeked Hornbill at Amani bred in the short rains (Moreau 1936). As the short rains appear relatively more important for breeding than the long rains in several eastern Tanzania localities, this may not be true for the Silvery-cheeked Hornbill generally. The 'breeding season' is established on the basis of only three records by Moreau (1936), which are still the only definite, dated records we have.

Thus, although all non-passerine forest fruiteaters tend to have rather widespread breeding seasons, repeating the relatively adaptable trend shown by forest non-passerine insect-eaters, they also tend to show a preference for breeding in dry months. Moreau (1936) has already commented, in regard to the Silvery-cheeked Hornbill, that a sharply-defined breeding season does not accord with the availability of some fruit, yearround; perhaps availability of food is less important than a breeding site unaffected by rains. However, the fact that both hole-breeders (hornbills and barbets) and those which make flimsy nests in trees (turacos and pigeons) tend to behave in the same manner, suggests that the breeding seasons of forest non-passerine fruit-eaters probably connected with optimum food supply. It is also known that barbets (e.g. Golden-rumped Tinkerbird) may have their holes soaked in heavy rains, while entire trees, branches or stumps may collapse. The young may be destroyed by driver ants Dorylus spp. which may

be more actives especially at night, in the rainy seasons.

Elliott (1950) drew attention to the possible importance of driver ants affecting forest birds. The hunting hordes of these ants flush insect food, that might otherwise be hard to find, into the waiting beaks of many insectivorous birds. On the other hand, these voracious ants can overwhelm a nest of young birds, even in a quite secure situation some distance above ground in a human dwelling (the Little Swift, Region E, L.H.B. pers. obs.). Driver ants become active just before and in the early rains, and are most active at night. Their effect on breeding birds, if any, should be most marked among those species that breed in the rains and near to the ground, where they would be most easily located and destroyed. However, the fact that most insectivorous forest passerines have a preference for the long rains in areas where driver ants are abundant, argues against the serious importance of driver ants as an additional hazard adversely affecting breeding. Certainly, the subject needs closer investigation before it can be accepted as having any marked effect on breeding seasons.

The forest passerines truly dependent on fruit (though some, at least, feed their young partly on invertebrates (Onychognathus spp., Brown 1965)) are mainly starlings. Among these the Slender-billed Chestnut-winged Starling, which feeds mainly on forest fruits, (especially of Trema and Ficus spp.) is unique, and breeds at a time when low flow in rivers permits easy access to the breeding site under waterfalls. Of the others, some breed both in rains and dry periods, but (in Region D) Stuhlmann's Starling shows an ill-defined peak before the short rains, rather resembling Sharpe's Starling and Abbott's Starling. From the scanty evidence, however, the Violet-backed Starling breeds in the early rains.

The most striking case of a defined breeding season is that of the Splendid Glossy Starling, with a very clear peak in March, the end of the hot dry season with a few showers. Two-thirds of all records are for March and 17/21 January-March. This species feeds on any available fruits, but possibly this well defined breeding peak is connected with abundance of a certain sort of fruit.

Bulbuls and greenbuls are generally poorly

documented, apart from a few not exclusively forest species. They show a stronger tendency than starlings to breed in the main rains, like forest insectivorous passerines. The Yellow-whiskered Greenbul, a relatively well documented insect and fruit-eater (van Someren 1956), has ill-defined breeding seasons in some areas, but in Region D has a definite peak in the long rains. The Zanzibar Sombre Greenbul in Region E has a peak in the main rains, but a second peak October-November, a warm period with occasionally some rain. Moreau (1950) has already drawn attention to a striking case of a number of pairs of Shelley's Greenbul laying almost simultaneously in the last week of August at Amani, where the species normally breeds in and after the short rains, November-February. Until more data are available on the food and breeding times of these forestloving pycnonotids, sound conclusions are impossible; however, it does seem that they are less dependent on the factors that lead to dry season, or short rains, breeding in starlings.

There are hardly any records for true forest orioles. The Black-headed Oriole which frequents forest near Nairobi—whence many of the records come—breeds mostly in rainy months, with peaks in both rains in Region D. None of the seed-eating Serinus spp. occurring in forest is exclusively dependent on fruit, and there is no exclusively fruit-eating turdid. Some species such as the Olive Thrush (not exclusively a forest species) eat much fruit as adults but feed their young mainly on insects. The Thick billed Seedeater, though poorly documented, evidently breeds in both rainy seasons.

Thus, most forest fruit-eaters—passerine and non-passerine—prefer to breed in the dry season, though forest greenbuls and some others tend to show a pattern resembling that of insectivorous forest passerines, with peaks in the main—or sometimes both—rains. Further study may show whether such patterns are due to increased dependence on insect food when rearing young.

However, it is clear that passerine forest fruiteaters tend to have a definite breeding season, usually not the same as that of insectivorous forest passerines. This season is centred on the dry season but is often rather ill-defined. Clearly, the same factors do not control both groups; the suggestion (Moreau 1950, Chapin 1932-54) that the equable forest climate necessarily leads to widespread breeding among most forest species is incorrect. This conclusion, expressed by Moreau (1950) as a percentage of the total number of forest species breeding in any month, clearly obscures the differing food preferences of forest fruit-eaters and insecteaters. When separated into two sub-groups, as here, these are found to breed at different times of the year, though the differences are less marked among non-passerines than passerines.

Group (3) Fish-eating Water Birds: These include the Great Crested Grebe and (to some extent) other grebes, pelicans, cormorants and darters, herons and egrets, apart from a few largely or exclusively terrestrial species, some storks (though again several are terrestrial and one mainly a carnivorous scavenger), two raptors (an eagle and an owl, discussed under that group) and some kingfishers. Other water birds, such as cranes, may eat an occasional fish but are not mainly piscivorous.

Many of the larger fish-eating birds show great breeding irregularities and seem decidedly opportunistic breeders, suddenly breeding in great numbers when conditions may be ideal, and, in other years, not breeding at all. Those with long breeding cycles, such as the larger storks and herons, may start to breed in wet conditions but rear their young in dry weather. It seems particularly important to try to assess what triggers breeding and at what stage of the breeding cycle food demand is at a maximum.

Mode of hunting for prey, and habits of the prey, are also relevant. Some (most herons, some storks) hunt prey in shallow water, clear or opaque; if they hunt by sight, as many do, clarity of the water is probably an advantage. Some, however, hunt mainly by touch in shallow water. Others, such as grebes, cormorants and darters, hunt by swimming and diving, often in deep water, while pelicans hunt whilst swimming in shallow water. These methods of hunting affect the range and size of fish prey that these birds can take. When such differing factors are considered, it becomes less surprising that there is very wide variation in time of breeding among species and from year to year within the same species.

The food of many species of fish-eating birds has not been quantitatively assessed in East Africa. It is therefore usually difficult—perhaps impossible—to assess breeding seasons in relation to the habits and local abundance of fish. As among raptors, the diet and feeding methods of fish-eating birds should be correlated with the populations, times of abundance, and habits of the fish prey and also with such factors as opacity of water following floods, which may temporarily make an abundant species of fish difficult to see and catch.

Allowing for such qualifications, the following applies to the various groups of fish-eating water birds:

- (i) The Great Crested Grebe, and two other not exclusively piscivorous grebes, breed in many months on permanent waters, but rain triggers dispersal to temporary ponds and lakes, and most nesting takes place late in or soon after rains. In Region D, the Great Crested Grebe breeds in both rainy seasons. Thus, the eggs are laid often in wet weather when water levels are highest, but young may be reared in dry weather when water levels are falling. Dry weather following rains may possibly coincide with maximum supplies of certain small fish and tadpoles in shallow water, while the water is relatively clear for diving birds that hunt their prey by sight. However, it remains to be shown whether the breeding season is controlled by weather conditions or by optimum food supply. Weather conditions certainly appear to trigger breeding in all three species, piscivorous or other.
- (ii) Pelicans: Breeding amongst the Great White Pelican occurs erratically (on the ground, in huge colonies) in seasons apparently controlled more by the inaccessibility of the breeding site than by any demonstrably abundant food supply. Breeding can be completely opportunistic, as at Lake Natron in 1962 (Brown & Urban 1969). In more regularly used sites, breeding apparently peaks in the Lake Rukwa swamps early in the dry season, but at a time of maximum inundation, making the breeding sites inaccessible. At Lake Elmenteita, Region D, it may be triggered by the presence of a colony of flamingos, continue for some years, and—for unknown reasons suddenly cease; or (as is usual in more recent years) it may begin in the long rains, reach a peak just after the long rains, and in some years continue with a second, lesser peak after the long rains, or in the short rains. The maximum food demand occurs

when both parents are feeding large young, some three months after egg-laying; thus, a laying peak in June at Elmenteita would mean that most food is needed in September, towards the end of the mid-year dry season, and also late in the dry season at Lake Rukwa.

The Pink-backed Pelican is a more regular annual breeder than the Great White, resorting to traditional tree sites in smaller numbers each year. It is not opportunistic. Though not fully documented quantitatively anywhere, at one well-known site, in Region B, breeding begins in August, late in the main rains, with young in the nest October-February. The peak food demand is about December, in the dry season. In Region D, peak laying is late in, or just after, the long rains, with the peak food demand again in the dry season.

These two pelicans hunt by different techniques, the Great White communally, by the 'scare-line' technique, catching the fish partly by touch; the Pink-backed usually singly and catching the fish by sight. Opaque water is probably unimportant to the Great White, but clear water should favour the Pink-backed. However, on available records, both have maximum food demands in the dry season in East Africa.

(iii) Cormorants and darters: The Cormorant breeds year-round, although peaks are not adequately brought out by available records. Further work may demonstrate peak laying in the rains, in some sites only in the rains, as at Lakes Abiata and Shala in the Ethiopian Rift (Urban, in prep.) The Long-tailed Cormorant shows clearer laying peaks in, and just after, the main rains, or at seasons of maximum inundation (Region C); it more often breeds in association with herons, egrets, and ibises. The African Darter may breed in association with Whitebreasted Cormorants at some sites, either alone, or with many species of herons, egrets and ibises. It breeds most often in the late rains or in the dry season; but, in areas of inundation, it breeds when high water makes the nest-site inaccessible, as in other species. In inundated areas, flooding makes for inaccessibility, but also probably increases the available food supply. Which of these two factors is more important in such sites has yet to be established. At permanent lakes during the dry season, clear water should tend to favour all these diving birds

which hunt by sight. At such times food may not be most abundant, but it may be more available. Further research is needed to establish the factors controlling all these species, all of which have a moderately long breeding cycle, lasting $2\frac{1}{2}$ -3 months.

(iv) All herons and egrets, including the terrestrial insectivorous Cattle Egret and the semi-terrestrial Black-headed Heron breed largely in the main rains, usually showing a very clear peak at the height of the rains or, in inundated areas, at the time of maximum inundation. Fish-eating populations of the Black-headed Heron, apparently conform to this pattern, while the more terrestrial populations breeding in towns may prefer the dry season. Even among these, however, those breeding in Nairobi showed strong laying peaks in the wettest months.

Most herons appear to be triggered to breed by heavy rain, or flooding of inundated areas. However, some (for example, the Grey and Purple Herons) are very erratic breeders, nesting in some years in numbers and then not at all, in the same area, for several subsequent years. Herons may also start breeding and then cease if there is a break in the rains, or if a temporarily flooded area dries out. In the semi-terrestrial Black-headed Heron, it seems likely that heavy rains result in abundant food supply, varying from year to year, which possibly regulates the numbers breeding in a traditional site in any one year. Even in this species, however, there are inexplicable examples of breeding in one year and not in others (for instance, in Malindi in 1976—but not in 1977, or 1978, or any known previous occasion).

In some other species, numbers breed in some years and none at all in others. Such an irregular opportunistic pattern is difficult to reconcile with variations in food supply, which are probably more regular and should enable some individuals to breed in all years, especially at such places as Lake Naivasha where *Tilapia* spp. are obviously abundant in shallow water, even in years when these herons do not breed. The amount and distribution of the rainfall thus seems more likely to regulate breeding of most herons than actual available food supply.

(v) Among storks and their relatives, the Shoebill is said to breed in the main rains in East Africa, but in both the Bangweulu Swamps of Zambia and in the Nile Sudd region (with rainfall patterns correspond-

ing to Regions C and A, respectively), it breeds during the dry season as the water in flooded grasslands recedes (Buxton et al. 1978; A.Guillet, pers. comm.). The lengthy breeding season of this species means that its maximum food demand falls late in the dry season, four or more months after egg-laying. The poorly documented Hamerkopby no means completely fish-eating-apparently also prefers dry season breeding. The largely fish-eating Woolly-necked Stork and Saddle-billed Stork for preference lay, or rear their young, in dry seasons, as does the mainly scavenging carnivorous Marabou, which also eats some fish. These partly or mainly fish-eating storks thus broadly contradict the tendency shown by herons to breed in the rainy season-or in times of maximum inundation-though the Shoebill lays when the flood waters are high in flooded grasslands.

(vi) Purely fish-eating kingfishers are poorly documented except for the Pied Kingfisher which, in Region B, breeds during a break in the main rains. Where such species breed in the banks of large rivers they must breed in the dry season, irrespective of food availability.

(vii) Those Laridae and their near relations which breed inland-the Grey-headed Gull, the Whiskered Tern, and the African Skimmer-all of which probably feed upon aquatic invertebrates, as well as small fish-show rather varied breeding seasons. In some cases, they are clearly associated with availability of the breeding site. In the Greyheaded Gull, most laying occurs late in, or just after, the long rains—a season coinciding with that of many non-piscivorous water birds, such as rails and ducks, but also with fish-eating grebes. The Whiskered Tern, with a shorter breeding cyclc, may breed in, or after, either rainy season, though apparently, in any one locality, laying peaks after one or other rainy season. The African Skimmer is clearly affected by the availability of a safe breeding site. On stable lake shores, it prefers the main rains, but on river sandbanks breeds in the dry season, when the water is low. These data suggest that food supply may be largely immaterial, though when the site is secure, breeding is apparently triggered by the rains, as in many other aquatic species.

Group (4) Other, non-fish-eating water marsh birds: These include an enormous variety of species, from some mainly terrestrial large storks and the Crowned Crane, to aquatic rails and ducks, ibises, plovers, snipe and such species as pratincoles and thicknees, which breed on sandbanks and on rocky islands. Among kingfishers, some species are birds of the waterside but are not wholly fish caters. In such a varied assembly, varying in size from that of a large crane to a very small plover (and in habit from purely aquatic to largely terrestrial), it would be most surprising to find any one factor largely controlling all of them.

Moreau's (1950, p. 260) generalisation about water birds (fish-eating and other) was that 'ducks and other water birds in most areas tend to breed in the later part of the rains and just after, when the watery areas are most extensive. No doubt the water birds by their timing secure the maximum food supply.' He considered that the breeding seasons of all water birds were probably timed to coincide with maximum food supply; but he had little direct evidence of this and stated (op. cit., p. 224) that his very large group of diverse species could be subdivided with advantage. We have here divided it into two, and comment below on further divisions of the varied large group of water birds which do not basically eat fish, but may feed on vegetation (including plankton) and/or mainly on invertebrates for the most part.

The smaller grebes, which may feed partly on invertebrates, have already been discussed; like the fish-eating Great Crested Grebe, they breed late, during or after, the main rains, and into the cool dry season. The Cattle Egret, largely terrestrial and an insect-eater, basically conforms to the pattern set by fish-eating herons, with which it often consorts in mixed colonies, but is somewhat more adaptable and may breed in dry as well as in wet seasons. Among storks, the terrestrial, largely insectivorous Abdim's Stork very clearly breeds in the main rains in most of its range, and, in East Africa, may begin breeding late in the dry scason and continue into the rains. The Open-billed Stork breeds at the height of the rains, or at periods of maximum inundation, often in company with other species of storks, ibises and herons. Its breeding dates have been correlated by Kahl (1968) with the emergence from

aestivation of the main food species, *Pila* snails. The Marabou eats some fish, but is mainly a scavenging carnivore. It lays mainly in the dry season, but (in Region D) also in the short rains; however, in all cases the breeding is timed so that the large, or recently-fledged, young are in the nest or leave it at the end of a dry season, when carrion is most likely to be abundant. In all three of these storks, including the terrestrial Abdim's stork, the breeding season apparently does coincide with the probability of abundant food supplies.

Among ibises, which feed largely by probing in soft ground or mud, the Sacred Ibis breeds at the height of the rains, or just after, resembling fisheating herons. The Hadada has a more elastic breeding season, peaking in and just after the main rains. The Glossy Ibis is curious in that, even in mixed heronries where most other species breed at the height of the main rains or inundation, it tends to breed later than other associated species. While there is no evidence to support such conjectures, it seems possible that its food supply might be most easily obtained in soft mud left exposed by receding water, or, alternatively, it is unable to compete for nesting space. The African Spoonbill, which also eats fish, breeds rather late in the main rains, basically resembling the Sacred Ibis but rather later, though often in association with it.

The two species of flamingos-of which the Greater Flamingo feeds on small invertebrates in the mud, and the Lesser Flamingo on blue-green algae or diatoms (Ridley, Moss & Percy 1955)-are very erratic breeders, not nesting every year. The Greater Flamingo at Lake Elmenteita may sometimes be triggered to breed by rainfall, but at Lake Natron it breeds mainly in association with the Lesser Flamingo, which nests most often during the October-December short rains; sometimes also in August (one huge colony biassing the figures). It is impossible to correlate these breeding dates with food supply or regular climatic data although, at Lake Elmenteita, the Greater Flamingo tends to show a breeding peak late in, and after, the long rains, while the Lesser breeds most often in the short rains at Lake Natron.

Most ducks and geese are rather poorly documented. The whistling ducks *Dendrocygna* breed mainly in the dry season; the Egyptian Goose during most of the year, with some preference for dry

months; the larger Spurwinged Goose and Knobbilled Goose (or Comb Duck) during and just after, the main rains. The Pygmy Goose prefers dry seasons, as do the Maccoa Duck and the Black Duck. Most Anas species and the Southern Pochard breed late in the rains and into the following dry seasons, the cooler mid-year dry season being preferred in Region D. The White-backed Duck, whose young live on chironomid larvae, also prefers the late main rains and cool dry season. In general, ducks tend to avoid the wettest months and the hottest months, but breed most often when the weather is relatively cool and dry and the water of breeding areas, though often quite stable, may be receding.

The Crowned Crane breeds most frequently in the rains in Regions A and C, with six months dry and six months wet. Where the rainfall peaks are bimodal, in Region D, it prefers the rains in the drier parts of its range, and the dry season in the wetter parts, Region B. It thus confirms the type of pattern shown by several other ground-breeding species. It is evidently dependent on wet weather in areas with a very long and severe dry season, while definite breeding seasons may be obscured by the tendency to lay repeatedly in the same site if a clutch or brood fails.

Many small skulking rails are poorly documented, but the majority of rails, whether purely or largely aquatic (such as the Red-knobbed Coot, or those largely frequenting dense fringing vegetation), tend to breed late in the main rains, or in the cool dry season following, in areas with two dry seasons. On scanty evidence, the Finfoot resembles the pattern of rails; the Jacana lays mainly in, or just after, the main rains. In regions with two dry seasons a year, the cooler season is selected. Almost all these birds-which breed in reedbeds or in vegetation floating on open water, where eggs could be easily flooded or chilled-avoid the wettest months for laying and the hottest dry months for rearing small young. Whether these preferences are also connected with variations in abundance of food seems problematical, since some species (Red-knobbed Coot, for instance) are largely vegetarian and others feed mainly on small invertebrates.

The Long-toed Plover and the Blacksmith Plover lay late in the rains and in the early dry season,

especially the cooler mid-year period where two dry seasons occur. However, the Spur-winged Plover breeds mainly in the rains, and the White-headed Plover, which breeds on exposed river sandbanks, lays at the height of the dry season. These variations appear more clearly correlated with climatic conditions and availability of nest site than with possible food supply. The Three-banded and Chestnutbanded Plovers both breed late in the main rains and into the following dry season, especially (in Region D) the cool dry season, avoiding the wettest and hottest months. Coastal records for the White-fronted Sandplover are all in the cool mid-year dry season, after the main rains. Kittlitz's Sandplover, on available evidence, shows a very unusual and apparently inexplicable pattern. In regions with two dry and wet seasons, it lays in and after the main rains continuing into the cooler dry season; but, in Region C, it breeds in the dry season and, in Region A (also with six months dry and six months wet), it breeds in the rains! More data are needed, but one possible explanation of this curious pattern is that the species avoids laying in the hottest months, breeding in the relatively cool rains in Region A, and in the comparatively cool dry season in Region C.

The available records show that snipe breed in the rains. Black-winged Stilts and Avocets breed in and after the main rains and, like many others of this group, prefer the cooler, dry season if a choice exists. They are very likely to have their nests washed out in storms (Reynolds, pers. comm.). The Senegal and Water Thicknees, on river sandbanks, breed at the height of the dry season; but, on Lake Victoria, where water levels are relatively stable, at the end of the rains, September-October. In coastal areas, the Water Thicknee avoids the wettest months.

The Commn Pratincole, a ground breeder, follows the common plover pattern of breeding late in the main rains and into the cool dry season. However, the situation may be more complicated than appears since, in Region C, its nesting grounds are drying flats exposed by receding floods, while at Magadi its main nesting ground is never flooded (Reynolds, pers. comm.). On the Nile, the White-collared Pratincole breeds in the dry low-water season and, on Lake Victoria, during the cool dry season, or in a break between main rains, avoiding the hottest and wettest months.

Other birds falling into this category include some kingfishers and bee-eaters, which may not be wholly or even largely dependent on a waterside environment, but happen to breed in river banks, and may obtain some food in, or over, water. The Redthroated Bee-eater breeds in the dry season in Region A; and so, in most authenticated records, does the Madagascar Bee-eater, in Region D. In one record, from Region B, however, this species is reported breeding in a river bank in the height of the rains! The Chestnut-bellied Kingfisher, both insectivorous and piscivorous, breeds during many months, with some preference for rains, even though breeding in river banks. The Malachite Kingfisher, which feeds on tree frogs as well as fish, breeds in banks mainly during the rains but may rear a series of broods in the same hole (Reyer, unpub.), even when successful—one brood following upon another. Better data for most kingfishers are needed before sound conclusions can be drawn.

Assessing the available data in general terms for this large and very varied group (many of which have not been studied in any detail in East Africa) we are struck by the fact that, excepting a few storks which may breed at a time clearly associated with optimum food supplies, a great many other species not closely related to one another, including ducks, rails, plovers and pratincoles, lay normally late in the rains producing young in the dry season. Where possible, the wettest and hottest months are avoided. If food supply were the principal factor affecting breeding seasons, one would expect some individuals of many of these species also to breed in the short rains in Regions B and D. A few sometimes do so (for example, Avocets), but most show a single definite peak during and after the long rains. This suggests to us that the climatic conditions prevailing may be more important for most of these species than food supply. A crucial factor may be cloud-cover, resulting in less direct solar radiation and lower ground temperatures (Reynolds, pers. comm.).

Group (5) Raptors: These include the order Falconiformes (hawks, eagles, vultures and falcons) and the order Strigiformes (owls), and vary in size from the Pygmy Falcon (weighing 65 grams) to very large eagles and vultures a hundred times as heavy, and from the tiny Scops Owl to very large eagle owls.

The diurnal birds of prey feed on everything from a dead elephant (as carrion) to alate termites. One species is even a vegetarian. Owls, however, eat no large carrion and even the largest species can scarcely kill anything heavier than a hare *Lepus* sp., weighing perhaps 3 kg. Most feed on living prey less than 1 kg in weight, down to small insects.

Moreau's generalisation on raptors was that most (especially, large) species lay in the 'cool dry season' and he also supposed that this would result in young in the nest when cover was reduced (often through burning) and prey was therefore easier to catch (Moreau 1950, p. 260). He omitted to note that, in the northern tropics, the dry season is also the hottest and sunniest season of the year, whereas, in the central parts of East Africa, the mid-year dry season between long and short rains is cool and overcast while, in the southern tropical rainfall regime (Region C), the dry season is also relatively cool compared to that in the northern tropics (Region A). Even supposing that dry seasons were always relatively cool, it is far from true to say that most raptors—perhaps especially larger species more frequently lay during these months. Some definitely peak in rainy months. In some species with very long breeding cycles, notably the Crowned Eagle, it has already been shown that the weather at the time of egg-laying appears to be unimportant (Brown 1952, 1955, 1966).

From detailed studies on several raptors, food preferences are quite well known. Accordingly, for some of these species, it is possible to relate known breeding times to times of maximum abundance of prey. The habits of the parent birds, especially at the nest, have also been the subject of detailed quantitative studies for some species and it is often known whether the female takes part in killing prey during the late fledging period—often, but not always, the case. It is thus possible, among raptors, to relate abundance of food supply and parental behaviour to breeding seasons with greater precision than in many species so far discussed.

In doing so, it is desirable to consider three stages of the breeding cycle where shortage of food may be critical (Brown, 1971), for they could affect different species to differing degrees:

(i) The first of these critical stages is when the female must lay. The clutch can vary from a

single egg weighing 2-3% of the female's bodyweight, to four or five eggs-and in some owls (Asio, Tyto) even more, weighing over 20% of the female's bodyweight. Obviously, the energy requirement is relatively less for egg production in a female Rüppell's Griffon, laying a single egg about 2% of her bodyweight, than is that of a small falcon, laying four eggs perhaps 20-25% of her bodyweight. Food supply at egg-laying may not be critical, though the main energy requirement is likely shortly before egg deposition. Nevertheless, species laying relatively large clutches generally breed more regularly-with a lower percentage of non-breeding pairs—than do large species laying small clutches. It seems rather unlikely that the food availability just before egg-laying is critical. Perhaps the hunting ability of the male, and his ability to feed the female just before egg-laying, may be more important than the actual amount of food available.

(ii) The next and most obvious of these critical stages is when the male is feeding himself, his mate and one or more large young, with appetites similar to, if not greater than, that of an adult. For about half to about two-thirds of the fledging period in most species—and in some species, during the whole of the fledging period the male is providing for three to five, occasionly more, adult equivalents. Any strain on his hunting ability, leading to brood loss through starvation, should appear now. Observations on well known species show, however, that very little brood loss occurs at this stage. Most occurs when the young are small and weak and their appetite much less than in the feathering stage, either through sibling agression (especially in eagles) or from other causes.

(iii) The third critical period occurs when the young become independent of their parents and are obliged to fend for themselves. Sometimes—for instance, in vultures and the Fish Eagle—they must compete directly with stronger, more expert and experienced, adults which, in Fish Eagles, may even rob their own young (Brown, unpub.) Heavy mortality from starvation might then be expected. In Europe and North America, observations show that

60-90% of young raptors die before they reach sexual maturity, most dying in their first winter (Brown & Amadon 1969). Though ringing studies are not available in East Africa, counts of adults and immatures of various ages in several species have shown that heavy immature mortality certainly occurs (Brown & Cade 1972, Brown & Hopcraft 1973) The stage at which the inexperienced young raptor is learning to fend for itself, in competition with adults living in the same area, may be the most critical of all for the survival of a stable population. For Rüppell's Griffon and the White-backed Vulture it has been suggested (Houston 1976) that the laying season is geared to the production of young, six or seven months later, at a time when food supplies are optimal for them, and competition with adults would thus be reduced.

The relation of laying dates and subsequent stages to food supply cannot be properly assessed for any species without considering these factors. Available data from detailed studies at the nest often enable an assessment of the probable effects of food shortage in a normally long (3–22 months) breeding cycle than for any other species.

Diurnal raptors may be divided into a number of sub-groups, related to prey preferences—for instance, insect-eaters; small mammal-eaters; small bird-eaters; large mammal-eaters; large bird-eaters; carrion-eaters/scavengers; snake-eaters and lizard-eaters; fish-eaters and a few specialist aberrant types (such as the Bat Hawk and the vegetarian Vulturine Fish Eagle). Although the Tawny Eagle and Bateleur take a wide variety of living prey and carrion, and may pirate prey from other species, they are considered here as members of one or other sub-groups.

The diurnal, largely—or wholly-insectivorous, species include the forest and woodland Cuckoo Falcon; the migratory Swallow-tailed Kite of arid lands; and the large, semi-nomadic Secretary Bird, which eats more insects than larger prey such as rodents and snakes. The Swallow-tailed Kite and Cuckoo Falcon are little known, but apparently breed in the rains; the Secretary Bird, breeding in both wet and dry months, peaks during or after both rainy seasons in Region D, the best-documented area. The four-month breeding cycle of the Secretary Bird, however, would mean a maximum food demand

late in the fledging period September—October or March-April, when cover is at a minimum, grass may have been burned, and grass-loving insects may be at a low level of population. Thus, its breeding periods, laying in or just after the rains, are not necessarily geared to maximum food demand, but could be related to availability of prey.

Small mammal-eaters include the rat-eating Blackshouldered Kite; two buzzard species; the Tawny, Wahlberg's and Long-crested Eagles; and the Greater Kestrel and Kestrel.

Adequate records permit good analysis for most of the larger species. The breeding season of Wahlberg's Eagle (laying August-November, peaking in late September and early October) is connected with the species' migratory pattern and nothing elsc; cover and rainfall conditions are immaterial. The young may be in the nest at the end of the rains, when cover is at a maximum, or (in western Kenya and Uganda) early in the dry season. This species, however, also feeds on game birds and reptiles. The Tawny Eagle-which again often kills larger prey, especially gamebirds-begins breeding in the main rains and peaks late in, and just after, the long rains in Region D. A similar pattern is shown in Region D by the Augur Buzzard in savannas between 1200 and 2000 m, but this species breeds only in the driest part of the year on montane moorlands, thus repeating the avoidance of the wettest months shown by some small montane forest passerines. The Long-crested Eagle and the Fox Kestrel, Kestrel and Greater Kestrel breed either definitely in the dry season in Region A, or mainly at the end of the long rains and into the subsequent cool dry season in Region D. These breeding seasons arc not necessarily connected with irregular cycles of abundance of grass rats.

Among small bird-eaters, we include the Harrier Hawk, which feeds much on the young of weaver birds; the African Marsh Harrier, three small accipiters and the Gabar Goshawk; Ayres' Hawk Eagle; the Red-necked Falcon and the African Hobby (which is partly insectivorous but feeds its young on small birds). They may conveniently be divided further into those of forest (Harrier Hawk, Ayres' Hawk Eagle and one Accipiter) and those of savanna or thornbush.

Most small forest passerines (group (1) of this discussion) prefer to breed in the long rains (where there are two rainy seasons) so that their populations should be at a maximum in May and June. In these same regions, the African Goshawk sometimes breeds late in or after the long rains, but still more often in, and just after, the short rains, when populations of its prey are not at a maximum. Ayres' Hawk Eagle lays mainly May-August and its time of greatest demand, with large young in the nest, is therefore August-November, when populations of small birds should be relatively low (though those of doves and gamebirds-sometimes taken-are likely to be high). In Region D, the Harrier Hawk shows a fairlyclear laying peak in the short rains, with young in the nest December-January, a time not in accord with peak availability of young birds. Thus, amongst forest species that eat small birds, breeding is often not correlated to peak periods of abundance of probable prey.

In the small accipiters, the Gabar Goshawk and the two small falcons of open country, most laying occurs late in the cool mid-year dry season in Region D. (in the case of the Red-necked Falcon in Region E, after the main rains). However, there are too few records from any region for these small birdeating species for any very definite conclusions to be drawn.

Of the large mammal-eaters, Verreaux's Eagle inhabits open country with rocky hills and 98% of its prey is rock hyrax. It breeds in the long, sixmonth dry season in Regions A and C and, in Region D, sometimes lays in the long rains but shows a peak in the mid-year cool dry season (with its maximum food demand late in that season), or in the subsequent short rains. While there is thus quite clear evidence that dry seasons are preferred by this species (the cool dry season, if there is a choice), there is no evidence that this preference is connected with abundance or availability of hyrax. Hyrax apparently breed all the year round (Sale, pers. comm.) and are perhaps always sufficiently common and easy to catch in the territory of a pair of eagles. On present evidence breeding appears to be connected with climatic factors rather than an abundance of prey.

The Crowned Eagle—a forest species, taking a wide variety of mammalian prey—breeds in Region

A (mainly Mau Narok) late in the rains; and, in Region D, shows a laying peak late in the cool, dry season, July-October, with its maximum food demand three months later, November-January when the cover is normally dense. In Kenya, it has an exceptionally long breeding cycle—up to 22 months. However, in this species the same female has been known to lay in June, July (twice), August and December—in all except one case rearing young to independence and suggesting that numbers or availability of prey is relatively unimportant. Though little data are available on the breeding seasons and relative abundance of prey animals, climatic factors appear to control the laying dates (Brown 1966).

Large bird-eaters include the Great Sparrowhawk, which specialises in pigeons and doves-(Brown, in prep.); the African Hawk Eagle and Martial Eagle, which feed largely on gamebirds; and the large Lanner and Peregrine Falcons. In Region D the Great Sparrow-hawk, lays mainly in the long rains and has large young in the cool dry season—a time which theoretically agrees with abundance of some large pigeons and doves. The available Region B records however, are for October, the end of the rains, and, in Region E, they cover July-October, a cool dry season. Thus, the same factors apparently do not affect all members of this species equally. The gamebird-eating Martial and African Hawk Eagles in Region D breed both during, or just after, the long rains in the cool dry season; elsewhere, the Martial Eagle lays mainly in the rains, the African Hawk Eagle usually in dry months. For both these eagles correlation between maximum food demand and greatest abundance of preferred prey is high. On scanty available records, the Lanner Falcon breeds in both dry seasons but the Peregrine shows a very clear peak in August. The time of maximum food demand for the Peregrine coincides with the arrival of large numbers of migrants from the Palaearctic and it is tempting to suggest that this largely aerial hunter may gear its breeding to this factor, as do Eleonora's and the Sooty Falcon elsewhere (Vaughan 1961, Clapham 1964). If the Peregrine is largely dependent on locally bred small passerines, however, it does not breed at a time of year when these are most abundant. Further study of its food preferences is needed.

Carrion-eaters and scavengers include vultures and the nearly omnivorous and highly-adaptable Black Kite, which is largely commensal with man. Four species of vultures have been studied in Region C, in the Serengeti plains, and provide valuable comparative data (Houston 1976, Pennycuick 1976). Of these, Rüppell's Griffon lays mainly December-January in the rains, and the young leave the nest August-September, at the height of the mid-year dry season when carrion is most abundant. Breeding was geared to produce young 6-7 months after egglaying, when carrion was most abundant and the young less likely to suffer from competition at carcases with their elders. In the same general area, however, both the solitary, tree-nesting Lappet-faced and White-headed Vultures lay mainly in the late rains and just after, April-July, so that they produce young markedly later than the colonial griffons. The relations of all these vultures at carcases have been studied by Kruuk (1967), who shows that, while the White-headed Vulture may be the main searcher, it is unable to compete with larger griffons, or the Lappet-faced Vulture who may follow it. Whereas the Lappet-faced Vulture is aggressive and able to rob other vultures of meat, it can also open carcases that smaller vultures cannot puncture. The breeding seasons of these two tree-nesting, solitary vultures do not appear, however, to be geared to maximum food availability for newlyfledged young, during September-October, as in Rüppell's Griffon and the White-backed Vulture in the same area.

In Region D, with two short rainy and dry seasons, the White-backed Vulture lays mainly during, and just after, the long rains, so that young are out of the nest in the following short rains. Since this species is apparently just as successful in Region D as in Region C, it is doubtful if the maximum availability of carrion is in fact the controlling factor dictating laying date (as Houston suggests). In Regions A and B, all large vultures breed in the dry season; but the breeding season of Rüppell's Griffon in the heart of its range in northern Kenya is not well-established.

Irrespective of weather conditions, the smaller, scavenging Black Kite breeds mainly November-March, beginning in the short rains in Region D and in dry weather in Regions A and B. It can

probably obtain food at any time of year and its breeding dates are primarily related to its pattern of movement, as in Wahlberg's Eagle. In Region D, the Egyptian Vulture lays late in the rains and into the cool dry season. The Hooded Vulture does the same in that Region, but definitely breeds in the hot dry season in Regions B and A. The specialised, bone-eating Lammergeier, with a very long breeding cycle, lays in the height of the rains in Region D, and (on the basis of but few records) in the dry season in Region A. These dates would tend to produce flying young at the end of the cool, dry season and early in the main rains, respectively. Since the Lammergeier is unable to compete with vultures or mammalian carnivores at carcases (Brown 1977), abundant supplies of bones—reducing possible competiton-may be important for survival of independent young.

Snake and reptile eaters include the snake eagles Circaetus, and the Bateleur, which also takes birds, mammals, and carrion; the two chanting goshawks Melierax spp; the Shikra and Lizard Buzzard; Dickinson's Kestrel; probably the Grey Kestrel and the Pygmy Falcon. No consistent pattern relative to the abundance or availability of lizards and snakes emerges from the scanty documentation. The snake eagles and the Bateleur lay mainly in dry months, though the Bateleur has a rather widespread breeding season. All have very long breeding cycles, so that the maximum food demand falls some four months or more after egg-laying during the rains. The two chanting goshawks lay during both dry seasons, rearing young during the rains, when lizards may be active. Interestingly the bird-eating Gabar Goshawk follows the same pattern, peaking late in the cool dry season, October. The Lizard Buzzard, Dickinson's Kestrel and the Pygmy Falcon however lay (on scanty data) in the cool dry season, rearing young at its end when the weather is hot and dry. Two records for the Shikra are for wet months and two for dry, and the only good record for the Grey Kestrel is late in the rains. In reptile-eating species, no very consistent pattern emerges to suggest that they can find food at most times of the year.

The fish-eaters include the African Fish Eagle, Osprey and Vulturine Fish Eagle (which is mainly

vegetarian in its main range but, in parts of East Africa, probably eats fish or crabs. We have rejected the only Osprey record, which (as Moreau (1950) observed) surprisingly agreed with the general pattern of land-based raptors. At Naivasha the Fish Eagle apparently prefers to lay during the rains; but in the wetter parts of its range, and especially where there is a clear alternative between long wet and dry seasons, it lays during the dry months and rears its young in dry weather. Even at Lake Naivasha, peak laying in April and May results in most young being in the nest during the cool dry season. For this, species detailed observations (Brown in prep.) at Lake Naivasha have shown that Fish Eagles on average spend less than two percent of daylight actually flying to hunt; and non-breeding pairs have little (or no more) difficulty in catching food than do breeding pairs in the same area. In this species, therefore, climatic factors appear far more likely to control the time of breeding than does the food supply.

Owls are naturally far less well known than are diurnal raptors, the best documented species being the large eagle owls Bubo spp. In these, the ground-breeding Spotted Eagle Owl and the Cape (Mackinder's) Eagle Owl respectively feed mostly on insects and rodents and they breed during or late in the dry seasons. In Region D, the Spotted Eagle Owl shows a clear laying peak July-December (especially September), which means that the large young are in the nest in the short rains. The time of maximum food demand would thus occur when the vegetation is dense and prey is not exposed to attack. Verreaux's Eagle Owl which breeds in old nests of other birds in trees and has a more varied diet-including insects, frogs, birds and quite large mammals, notably the hedgehog Atelerix (Brown 1965b)-has a more extended breeding season. but it still lays mainly late in the long rains, or in the cool dry season following. Its large young are in the nest, and becoming independent, late in the dry season and the short rains. In Region D, the normally rodent-eating Barn Owl (which also eats birds in some areas, C.-van Someren. pers. comm.) lays chiefly June-September, while the Grass Owl and Marsh Owl, breeding on the ground, lay at the end of the rains or in dry months. The few records for Woodford's Owl suggest that it breeds mainly late in the cool dry season in Region D. Smallcr owls are basically undocumented, but males of the Sokoke Scops Owl—presumably insectivorous and whose nest remains undetected—are most vociferous in May, at the height of the rains (P.L.B. pers. obs).

Thus, Moreau's basic generalisation—that the raptors, especially the larger species, concentrate breeding in the cool dry season—is true in some cases but not in all. Some of the largest vultures and eagles lay chiefly in the rains, as do some other species. Further data from Regions A and C, at present less well-documented than Regions B and D, will probably show that, in areas with long single dry and wet seasons each year, most raptors lay in the dry season, though Rüppell's Griffon in Region C is already a notable exception to this prediction, laying soon after the onset of rains to produce young seven months later. Evidence that the laying date of many raptors is geared to the production of young at a time when food supplies are most abundant is clear in but a few species; in others, it is, at best, shaky, while in many, the breeding season appears more likely to be associated with climatic factors than abundance of prey.

Raptors, in general, provide only rather limited support for the generalisation that, given a secure nesting site, birds will tend to breed at a time when food supplies are optimal for rearing young. Critical examination of the stages of the breeding season when food supplies are likely to limit success or survival shows that different species are affected in different ways, and that commonly, abundance or availability of food may be of lesser importance than other factors, especially climatic. But (for instance, in the Black Kite and Wahlberg's Eagle), the timing of movements, themselves largely dictated by weather changes within our region as a whole, assume importance.

Group (6) Ground-dwelling seed-eaters (not forest species): Among non-passerines these include francolins, quail, and guineafowl; some button quails are—at least partially—grass seed-eaters; and sand-grouse. Among passerines, larks feed partly upon seeds, especially the short-billed sparrow-larks Eremopterix spp. of arid country, but perhaps they feed their young chiefly on insects (van Someren 1956, Reynolds pers. comm.). Only a few other

passerines (such as the Quail Finch and Cinnamon-breasted Rock Bunting) are really ground-dwelling seed-eaters. Many other seed-eaters, passerine and non-passerine, necessarily feed on the ground but do not nest, rest or roost there.

With some exceptions, most francolins tend to breed in or just after the rains when the grass is green and long. This applies for example to the Coqui, Montane Red-winged, Red-winged, Hildebrandt's and Heuglin's Francolins; and the Rednecked, Grey-breasted and Yellow-necked Spurfowls. Shelley's Francolin, however, breeds in dry seasons both in Regions C and D and the montane Jackson's Francolin clearly breeds in the driest season of the year suggesting that climatic factors here override others. However, most francolin records are indefinite, since they usually depend on active broods, imprecisely aged, and not upon eggs. Better data are needed, but it is reasonable to assume that francolins breed in dense cover, protecting both the sitting female and small young from avian predators.

In quails, the montane Quail shows peaks both in dry and wet seasons but prefers the dry months, and the Harlequin Quail is apparently a nomadic opportunist breeder, nesting in numbers locally in response to favourable rains. The Blue Quail (few records), breeds late in the main rains. The only record for the Stone Partridge Ptilopachus refers to the dry season. Guineafowl (Numida and Acryllium) breed both in and just after rains, though again records are often hard to date. Unlike many species of passerines (with a shorter breeding cycle), guineafowl tend to breed in both rainy seasons, with peaks roughly proportionate to the amount of rainfall.

Virtually all gamebirds (with one or two exceptions, such as Jackson's Francolin) breed in the rains when cover is dense, and produce their young when seed crops are abundant. The food supply of three common species of gamebirds has been studied by Swank (1977), who found that the diet of all three was predominantly bulblets of sedge *Cyperus* spp., especially in the dry seasons. Stronach (1966) also found that the Yellow-necked Spurfowl ate *Cyperus* corms in Tanzania. Helmeted Guineafowl ate most sedge bulblets and Crested Francolins least. Crested Francolins ate most insects (31.8% year-round cf. 6.4% in guineafowl); but all species took some insects, and insects became most important to

Yellow-necked Spurfowl and Crested Francolins when the vegetation was green, soon after the rains. This suggests that, at least in smaller gamebirds, insects may be more important in the diet than is generally supposed. In the relatively insectivorous Crested Francolin, correlation between climate and laying date is less clear than in some other species; but—in some areas—it, too, shows peaks in the rains. Its main insect food is termites, likely to be abundant for much of the year.

In Button Quails *Turnix* (which may not be mainly seed-eaters), scanty records suggest peak breeding in and just after the main rains, resembling francolins. If they are not so dependent on seed supplies, this would be rather surprising. In Region A, the Black-rumped Button Quail apparently peaks June–July, a slightly drier break in the main rains. Good records for the Quail Plover are lacking.

Sandgrouse Pterocles spp. show a far clearer preference for dry-season breeding. All breed in the height of the dry season, or, at the earliest, the end of the rains. In Region D, with two dry seasons per year, the cool mid-year dry season is preferred by the Chestnut-bellied, the Black-faced and the Yellow-throated Sandgrouse. Sandgrouse thus breed decidedly later in the dry season than do francolins or guineafowl. As most are birds of arid country with less ground cover at any time of year, their breeding dates may be more specifically correlated with food availability than in gamebirds but a preference for the cool dry season may also be due to low ground temperatures (Reynolds, pers. comm). Additional studies are needed, particularly on the food taken by young sandgrouse.

True ground-dwelling passerines which are dependent on seeds are few. Larks may eat seeds when adult, but insects or invertebrates are certainly important in rearing young. In virtually all larks, including the more exclusively seed-eating sparrowlarks *Eremopterix*, there is a strong preference for breeding in the rains. Of *Mirafra* spp. the Singing Bush Lark, the White-tailed Bush Lark, the Rufousnaped Lark, the Fawn-coloured Lark, and the Pink-breasted Lark breed mainly, or only, in the rains with (in the well-documented Rufousnaped Lark in Region D) a strong preference for the long rains. The exceptions to this general rule are the Flappet Lark, with ill-defined seasons, and the

Dusky Bush Lark, with a single record in the dry season. (However, records for these species are inadequate). The Spike-heeled Lark breeds in both rainy seasons and all three Calandrella species breed in the rains in our Regions A, B and D, though in Zambia (and possibly in Region C, from which we have no records), the Red-capped Lark is a dry season breeder. The only records for Galerida spp. and the Short-tailed Lark are in or near the rains. In Region D, the sparrow-larks, Eremopterix breed in the rains, but, in Region C, where the rains and dry season are each longer and the ground more liable to waterlogging in the rains, they breed in the dry season. Thus, with this one exception, larks which might be expected to need dry ground for nesting—breed in the rains, a time when seed supply is least. However, since larks feed their young largely on insects (Reynolds, pers. comm.) an abundant seed supply is probably unimportant for them.

The few other ground-dwelling seed-eaters are little-known, but the Quail Finch breeds in the rains, while the Cinnamon-breasted Rock Bunting breeds in the rains in Region D but in the early dry season in Region C. Thus, most ground-dwelling seed-eating passerines breed entirely in, or just after, the main rains, suggesting that an abundant food supply of seeds is unimportant for breeding yet there are a few exceptions (*Eremopterix*, *Emberiza*) to indicate that, where rains are heavy and prolonged, the dry season will be preferred; though these same birds prefer rains-breeding in drier areas which have two short rainy seasons a year.

Group (7) Other Ground Birds: Among non-passerines, these include very diverse types, starting with the supposedly omnivorous but largely vegetarian Ostrich; bustards, plains-loving plovers (Vanellus spp.), thicknees, and coursers, all of which may eat many invertebrates picked up from the ground; and the exclusively insectivorous nocturnal nightjars.

Throughout, the Ostrich breeds in the dry season and in Region D, prefers the mid-year, cool dry season. Although more data are required from some other regions, it appears that the availability of a safe breeding site not liable to waterlogging is more important than any other factor. In Region D, near

Nairobi, the hatching of the chicks often coincides with the availability of fresh green vegetation, but this does not necessarily apply in Regions C and A, with their long hot dry seasons, or in the arid, northern parts of Kenya. Leuthold (1977) has shown that, in Tsavo (Region D), breeding occurs in both rains. At present, the breeding season of the Ostrich appears more likely to be directly geared to climatic factors than to food supply.

The records for bustards are usually scanty, but the large Kori and Denham's Bustards prefer the dry seasons—the latter showing a very clear peak in the late dry season in Region A. The smaller species breed both in wet and dry months; the records for the White-bellied and Hartlaub's Bustards are all in the rains while the arid bush-loving Crested Bustard breeds in both wet and dry months. The Black-bellied Bustard which tends to inhabit tall grass woodland with higher rainfall than the others of its genus, breeds at the end of the dry season, like Denham's Bustard in Region A. Thus, most bustards prefer dry months for egg-laying although for Denham's Bustard the chicks would be growing up in the early rains; and those of more arid areas or dry savannas and plains (the Crested, Hartlaub's and White bellied Bustards) may prefer to breed in the rains when cover is dense. Again, the intensity and timing of wet seasons appears likely to override food supply as the main controlling factor, though the food of bustards-and, indeed, their general habits-is surprisingly little known. Most are apparently largely insectivorous, so that dry season breeding is the more surprising.

The Spotted Thicknee, in Region D, tends to breed in both rains; but in Regions C and A, where rains are more prolonged and intense, it lays in the dry season. Records for most species of coursers are rather scanty, but indicate a clear preference for dry season breeding in most areas with, in Region D, a preference for the mid-year, cool, dry season. Any records in the rains are for species of dry country, Temminck's and Heuglin's Coursers.

The plains-loving plovers *Vanellus* spp. are among the best- documented of all ground-nesting birds. The Black-headed, Senegal, Black-winged, Crowned and Wattled Plovers all show a preference for dry season breeding in higher rainfall areas (Regions A, C and B) while the Black-headed and

Crowned Plovers definitely peak in, and just after, the main rains in Region D. The Black-winged Plover lays in the dry season in Region C (though better data are needed) early in the rains in Region A (Mau Narok), and at the end of the dry season, perhaps after the first showers, in Region B. This species generally inhabits higher, colder areas than the others, where the rainy season may be very cold and the ground easily saturated. These plovers thus show more clearly than any others that climatic factors can be of critical importance in the timing of the breeding season, sometimes meaning that a species lays at a time of year perhaps not optimal for its preferred food supply, in these cases insects, molluscs, and other invertebrates.

Nightjars are among the few purely insectivorous species breeding on the ground. Most breed only (or mainly) in dry seasons, but a few also breed in the rainy months, most records for the Fiery-necked Nightjar being for the rains, while the Slender-tailed Nightjar breeds in the rains in regions B, D and E and, in Region B, during a break in the rains. The Long-tailed Nightjar breeds during the dry season in Region A, but sometimes during the rains in Region B. Again, the records show that the preference for the late dry season is more marked in Regions C and A (Macrodipteryx spp. and the Long-tailed Nightjar) than in Regions B and D (the White-tailed and Montane (Abyssinian) Nightjars). Since the flying insects on which nightjars feed are certainly more abundant in, and after, the rains (as anyone who has spent a night in the bush with a paraffin lamp knows), this appears to be another clear case where ground-nesting forces upon the species concerned the need to lay at a time when food supplies are apparently not optimal. Climatic factors affecting available nest sites again override food supply in controlling breeding seasons.

The Hoopoe feeds largely on the ground and sometimes breeds in holes in the ground, and barbets of the genus *Trachyphonus* breed in holes in banks or (d'Arnaud's) in vertical burrows in flat ground. The Hoopoe breeds in the dry season and short rains in Region D and in the dry season in RegionB and C. Itmay be easier to excavate food when the ground is dry (C.-van Someren, pers. comm.). The two ground barbets prefer breeding in the rains in Regions A and C₂; but in Region D the Red &

Yellow Barbet prefers the dry season, with some breeding in the rains. Records for these barbets, however, are rather unsatisfactory, owing to the difficulty of establishing the contents of holes, especially in d'Arnaud's Barbet. They suggest that breeding in holes helps to eliminate the climatic hazard which appears to affect many other ground-breeding non-passerines.

Among passerines, wagtails Motacilla spp. which are normally partly or wholly associated with water, show ill-defined breeding seasons, perhaps because food supply is no problem, while they may also nest in sheltered sites. With few exceptions, pipits and long-claws Anthus and Macronyx spp. breed during, or late in, the rains, when the grass is long. Even the montane Sharpe's Longclaw breeds during the rains-contradicting a trend shown by some other montane passerines, of avoiding the coldest wettest months. A note-worthy exception to the general rule of rains breeding is Richard's Pipit in Region C, where the records indicate breeding mainly August-September, the hot pre-rains period. Insects may then be plentiful though sites secure from flooding are not. In view of the clear preference for rains-breeding shown by all other pipits and longclaws, even in regions likely to suffer the same climatic effects, the need here is for careful study and fuller records.

Few other passerines are, properly speaking, ground birds. Two wheatears, Schalow's and Capped Wheatears, breed in sheltered ground sites, often in banks, where wet may be less likely to affect them. Schalow's Wheatear has ill-defined breeding seasons but the driest months (August-September) are avoided and there is a peak early in the main rains. The Capped Wheatear breeds in the rains in Region D, but at the end of the rains and in the dry season in Region C, confirming a trend shown by some other species-for instance, Fischer's Sparrow Lark and the Red-capped Lark among passerines and a general trend noticeable among many nonpasserines—of avoiding very wet conditions for ground nesting. The two burrow-breeding turdids, the Anteater Chat and the Sooty Chat both breed mainly in the rains, suggesting that flooding of their burrows does not present a problem (as it apparently does for the Grey-rumped Swallow). In this respect, they rather resemble the unrelated ground barbets Trachyphonus spp. The Cliff Chat and the Little Rock Thrush also breed in sheltered sites among stones or in hollows and the few records suggest that they breed in the rains.

Surveying in general the other ground birds of this group, and regarding larks as possibly more dependent on insects for breeding purposes, there is a striking contrast between a very definite preference for breeding in the dry season (rarely or never in the rains) among a very diverse selection of groundbreeding non-passerines, from the Ostrich to purely insectivorous nightjars, and a very strong preference for breeding in the rains, often the main rains or wettest part of the year among larks, pipits and longclaws. There are cases both among non-passerines (e.g. Vanellus spp.) and passerines (Eremopterix, Calandrella) where the likelihood of very wet conditions, making nesting difficult, appears to override other factors possibly conducive to optimal food supplies. Breeding in holes in the ground in both Trachyphonus barbets and several wheatears and chats seems to enable a species to breed in the rains, although dependent on a ground breeding site. Except in gamebirds and buttonquails, it appears that in most ground-breeding non-passerines, climatic factors are more crucial than food supply.

One obvious difference between most passerines and most non-passerines breeding on the ground is the fact that passerines normally make a solid, warm, well-lined nest, or breed in burrows and sheltered sites (sometimes both) whereas most of the non-passerines breed right in the open with little if any nest. Gamebirds (breeding in dense grass cover), with some of the smaller bustards, may prefer to breed in the rains because of the nature of the cover in which they nest. More attention might be paid to the amount of nesting material used by gamebirds and the type of site selected (raised, on well-drained ground, etc.). Gamebirds are normally considered to be mainly seed-eaters though some are more dependent on insects than has been thought. They may be obliged to accept climatic hazards to obtain an optimum food supply. Among many ground-nesting non-passerines, especially among nightjars, it appears that ground-nesting forces the acceptance of a poor (or less than optimal) food supply. Among ground-nesting passerines, however,

perhaps the construction of a solid, warm nest enables most species to make use of an optimum food supply when climatic conditions could otherwise prevent this.

Group (8) Grass-dwelling seed-eaters and (9) Grassdwelling insect-eaters: Moreau (1950) listed only passerines (warblers and ploceids) as grass birds, and there are no non-passerines other than coucals which properly belong here, though there are several grassland birds which feed and nest on the ground (already discussed under ground birds). Typically, grass-dwelling seed eaters and insectivores attach their nests to grass stalks which are insufficiently robust for most non-passerine nests. All Euplectes and Quelea spp. and a few estrildids (e.g. Fawnbreasted Waxbill) are grass dwelling seed-eaters, though many take insects as well as seeds, especially for the young, and they may not all breed in grass. The Tawny-flanked Prinia, Fan-tailed Warbler, Moustached Warbler, Marsh Tchagra and most Cisticola spp. are grass or sedge-dwelling insecteaters, including swamp-edge species like the Winding Cisticola. The poorly documented denizens of the interior of Typha and papyrus swamps are rather atypical, in that the tall sedges and reeds they inhabit are less seasonal than those on dry or seasonally inundated ground. Nevertheless, both the insectivorous Lesser Swamp Warbler and the graminivorous Grosbeak Weaver have breeding peaks in the rains. The swamp, or swampedge coucals, the Black and Blue-headed Coucals, have rather flexible seasons, while the breeding of others, the White-browed and Senegal Coucals, peaks in both rains. Irrespective of food preferences, birds which attach their nests to the stalks of seasonal grasses are constrained to breed when the grass is long, in and after the rains. Some, for example Prinia spp., the Cardinal Quelea and the Red-faced Cisticola often attach their nests to stout vegetation rather than to grass itself (C.-van Someren, pers. comm.).

It is likely that, coincident with the availability of nest sites, insects will be most abundant in and after the rains. Apart from the *hunteri-chubbi* group (which typically occupy secondary growth forest, bracken-briar or heath), cisticolas show clear breeding peaks in the rains, especially the long rains in

bimodal rainfall areas, including the Tinkling Cisticola of montane bogs, though the seasons of the montane Aberdare Cisticola are poorly-defined. The Tawny-flanked Prinia and Marsh Tchagra breed mainly in the long rains, with Prinia breeding prolonged into subsequent dry months when grass is long; but both the Fan-tailed Warbler and the Moustached Warbler have rather ill-defined seasons, with only a tendency to breed in the long rains.

With a proportion of their diet prolific only when grass is long and flowering, seed-eaters (especially Quelea spp.) might be expected to have a still-more-defined season than these warblers. The breeding of Euplectes and Quelea spp. is in the rains or late rains, especially the long rains, though the Fan-tailed Widowbird and the Fire-fronted Bishop breed in both rains. The Zanzibar Red Bishop and the Yellow-mantled Widowbird have peaks late in the rains, or in the dry months immediately following. The few data for the Yellow-crowned Bishop, the Black Bishop and the Marsh Widowbird suggest that their seasons are rather ill-defined. The elaborate nuptial dress of Euplectes spp. provides a further potential constraint on their breeding seasons. Recent data from Karen suggest that the Red-naped Widowbird males, which sometimes exceptionally heavy short rains breed during December-January, might not be able to assume suitable plumage for successful display in the following long rains in April (Brown in prep.). An abundant seed supply following good short rains is not reflected in proportionate numbers of breeding pairs or displaying males in the Red-naped Widowbird.

Group (10) Miscellaneous seed-eaters: This category includes all non-forest estrildids and ploceids, other than those dealt with in group 8, as well as all Serinus spp. (though few of these are wholly graminivorous). With the exception of the Brimstone Canary which often feeds on fruit, Serinus spp. breed mainly in the rains, especially the long rains; the good data for the Streaky Seed-eater show clear peaks in both rains though at high altitudes it probably avoids breeding in the rains. Ploceus spp. breed mainly in the rains, favouring the long rains, though seasons may be prolonged, with records in all months. Some such records are probably corre-

lated with unseasonal rain in particular, the Black-headed Weaver which often shows an immediate breeding response to heavy rain, even if only a single shower, though such colonies often disperse before any eggs are laid. The colonial dry-country ploceids of the genera *Bubalornis*, *Dinemellia*, *Plocepasser* and *Pseudonigrita* also breed mainly in the rains, especially the long rains, and the few pre-rains records were probably in response to localized early rain.

Sparrows (Passer and Petronia spp) are probably not well placed here, as the diet of many may well be mainly insects. The few Petronia records are rather inconclusive, but Passer breeding is mainly in the long rains. Contradictions in the Grey-headed Sparrow are perhaps explained by its loose association with man. Virtually all Estrilda Uraeginthus and Lagonostica, spp. exhibit clear breeding peaks in the rains, particularly the long rains, though there ares subsidiary short rains peaks in the Red-cheeked Cordon-bleu, (Region B), the Waxbill, (Regions B and D) andthe Yellow-bellied Waxbill (Region D). The Crimson-rumped Waxbill and the grassland Fawn-breasted Waxbill have ill-defined seasons and the data for the Bronze Mannikin are remarkably random. Other Lonchura spp. breed mainly in the rains, and the late peak in the Silverbill no doubt results from its habit of utilizing abandoned ploceid nests, as is the case with the Cut-throat and perhaps the Zebra Waxbill.

The flowering grasses, in and after the rains, together with a flush of insect life, provide optimum food supplies in, and after, wet periods (and perhaps immediately before, in the case of insects). Although breeding seasons undoubtedly coincide with these times of abundance, a plentiful food supply does not always, or even often, result in proportionate numbers of individuals breeding.

Group (11) Miscellaneous fruit-eaters: This category includes all mousebirds and non-forest starlings and pycnonotids. The seasons of the starlings are rather diverse. The Red-winged Starling has a prolonged Region D season from October (before the short rains) to March (at the beginning of the long rains). Lamprotornis spp. are poorly documented though there is evidence of long and short rains breeding in the Blue-eared Glossy Starling, Rüppell's Long-tailed Glossy Starling and the Black-breasted

Glossy Starling; the three records for the Lesser Blue-eared Glossy Starling are in the long rains. Spreo spp., eating insects and berries in arid and semi-arid areas, breed mainly during the rains, including the short rains (which are heavier and more reliable in much of the eastern Kenya plateau, whence many of the region D records originate). Most pycnonotids have been dealt with under forest fruit eaters, and very few belong here. The good data for the Common Bulbul show that its breeding is linked with the rains, especially the prerains and early rains in regions B and C, the short rains and the subsequent dry season in parts of region D, the long rains in other parts of region D, and prolonged rains in region E. Yellow-throated Leaflove seasons are difficult to evaluate in region B, with peaks in the dry months December-January and in both rains.

In attempting to interpret the breeding seasons of this group in terms of food supply or other factors, one is struck by the diversity of patterns. Certainly, the rains are important in several species, perhaps especially in arid or semi-arid areas and in those species which eat predominantly insects, or at least feed their young mainly on insects. Breeding in the warmer pre-rains and short rains periods may be linked with local abundance of fruit, especially in starlings (the Red-winged Starling here repeating the pattern shown by the Splendid Glossy Starling and Cinnyricinclus spp. among forest fruit-eaters). Although there is insufficient information on fruiting trees, the general impression is that fruit is most abundant in the dry season, not in the rains.

Group (12) Miscellaneous, all others: This diverse assemblage contains a large number of mainly insectivorous species from many families, including all or most non-forest representatives of some families or sub-families. The relatively few non-passerines include cuckoos, rollers, bee-eaters and some kingfishers. Of the passerine families or sub-families with few species, oxpeckers have ill-defined seasons, probably because of year-round availability of food on stock or game. Crows show a tendency to breed in the hot pre-rains periods or during rains themselves, though the introduced Oriental Indian House Crow breeds in dry hot weather at Mombasa, with clearer seasonality than many birds in East

Africa (see species account). Cuckoo-shrikes, orioles (mainly the Black-headed Oriole) and drongos (mainly the Drongo) breed mainly in the rains. Tits (mainly the White-bellied Tit) have rather ill-defined seasons, but peaks in both rains. Babblers breed mainly in the rains or in the pre-rains periods (least defined in the Northern Pied Babbler and the Rufous Chatterer), and the two records for the Spotted Creeper are in wet and dry months.

Amongst non-forest flycatchers, the Swamp Flycatcher breeds mainly in the long rains, but has a clear short rains peak too, which is unusual in Region B. There is virtually no Region B short rains breeding in the Black Flycatcher, more typical in this respect. The rather ill-defined season of the Grey Flycatcher peaks in both rains in Region D, but most of the rains-breeding records for the Pale Flycatcher are in the long rains. The Silverbird breeds in the rains in Region C (few records elsewhere). The Chin-spot Puff-back Flycatcher breeds in the hot pre-rains and early rains in Region C. and in both rains in Region D, but October-February (in and around the short rains) at Arusha. Within Region D, a similar variation is especially clear in the Paradise Flycatcher breeding around Nairobi in the long rains but favouring the short rains and dry season in north-eastern Tanzania, at Arusha and elsewhere. The similar insectivorous, non-forest warblers breed mainly in the rains, especially the long rains. In addition to rains-breeding, there is a September-October peak for the Yellow-breasted Apalis just before the short rains. The feeding habits (systematic searching) of Sylvietta spp. might explain their relative lack of seasonality (mainly the Red-faced Crombec), although the ill-defined seasons of the Yellow-bellied Eremomela are more surprising.

The thrushes may be conveniently grouped as grass-dwelling and thicket-dwelling. In the first category, the Stonechat occupies grasslands and shrubbery at medium and high elevations and breeds during both rains, while the Hill Chat favours dry months for breeding at still-higher elevations on Afro-alpine moorlands. With the exception of the African Thrush which perhaps is better placed as a fruit eater, with a curious December-May breeding season in region B, thrushes of the genera Cercotrichas, Cichladusa, Cossypha and Turdus breed mainly in the rains, or in the hot pre-rains in region C.

The Lanius shrikes are typically 'pouncers', feeding on larger insects which they catch from prominent perches, usually in open woodland or savanna, though Mackinnon's Shrike is usually associated with forest edges. The dry-country Taita Fiscal and Somali Fiscal breed mainly in the rains, but others have less defined seasons. Nevertheless, the well documented Fiscal breeds in the rains and pre-rains in regions A and C, and in the long rains in region B, while the numerous records for region D show peaks in both rains. Shrikes of the genera Tchagra, Laniarius and Malaconotus live close to the ground in thickets, forest and wooded savannas. All tchagras breed mainly in the rains, especially perhaps the dry country Rosy-patched Shrike and the Threestreaked Tchagra, and there are clear peaks for the Brown-headed Tchagra early in the rains. The Tropical Boubou and the Slate-coloured Boubou breed mainly in the rains, though the latter has a prolonged October-May season in Region C. The few data for the Grey-headed Bush Shrike and the Sulphur-breasted Bush Shrike show no consistent pattern.

Hirundines feed on aerial plankton and breed mainly in the rains when food is likely to be most plentiful. Breeding behaviour and nest building of several Hirundo spp. is stimulated by the onset of rains which provides the mud necessary for their nests (and probably increases food supplies too). The more flexible seasons of some species might be explained by their association with human settlements where the availability of mud and food is likely to be less strictly seasonal. Amongst holenesting Riparia and Psalidoprocne spp., the Banded Martin and the African Sand Martin breed in the rains, with the exception of the latter in Region C, and the White-headed Roughwing breeds mainly in the rains. The Black Roughwing has ill-defined seasons peaking in the short rains in Region D. Availability of food supply here appears to override security of nest sites from potential flooding, except in region C, where rivers flood regularly rather than erratically (as is often the case in region D). Not all breeding is in river banks. Flooding is, however, of overriding importance in the unique ground-nesting Grey-rumped Swallow which breeds in dry weather (see Group 6).

The proportions of insects and nectar in the diet

of sunbirds varies immensely from species to species, and probably seasonally within a species, as has been demonstrated for the Scarlet-chested Sunbird in Nigeria by Pettet (1977). All or most Anthreptes spp. eat more insects than nectar but most of these are forest or forest-edge birds, and only the Uganda Violet-backed Sunbird and the Violet-backed Sunbird properly belong here, both breeding mainly in the rains, including the short rains. Seasons of the longer-billed and more typically nectar-feeding Nectarinia spp. are often ill-defined (for example the Amethyst, Scarlet-chested, Little Purple-banded and Mariqua Sunbirds), but some species have clear breeding peaks in one or both rains (for example the Copper, Mouse-coloured and Bronze Sunbirds). Since nectar from indigenous trees is probably available less at the height of the rains than at most other times, species favouring the rains for breeding are likely to be those which prefer to feed their young on insects. Nectar may be important to bring adults to breeding condition in some species, but seems unimportant for rearing young. Sunbirds breeding at high altitudes (above 2000 or 2500 m) often have regular altitudinal movements to lower dryer levels when high mountains are cool and wet. Nevertheless, seasonality is not especially marked in this group, though the Malachite, Scarlet-tufted and Golden-winged Sunbirds evidently breed mainly during dry weather.

Group (13) Seabirds: These include the Masked Booby, Sooty Gull and seven species of terms Sterna and Anous. Apart from Latham Island, some 60 km out to sea from Dar es Salaam, all known breeding colonies are on islands close to shore relatively-easily accessible even with small canoes. Until very recently, none of the known colonies has been readily accessible to more powerful motor-driven vessels and most were seldom visited before the 1950s.

The breeding seasons of seabirds on the offshore islands have been thoroughly discussed by Britton & Brown (1974). The Sooty Gull Larus hemprichi breeds in July and August, at the height of the south-east monsoon, when seas are rough and the small islands on which it breeds are least-accessible. However, it feeds mainly on the eggs and young of the several species of terns which share the

breeding islands, so that in this case there is evidence that the breeding season is timed to coincide not only with inaccessibility, but also with optimum food supply; this food supply itself depends on the inaccessibility of the islands.

On the offshore islands, the Common Noddy the Roseate, White-cheeked, Bridled and Sooty Terns, lay in July and August, when the islands are most inaccessible. The best documented species—the Roseate, White-cheeked and Bridled Terns—lay mainly in August; and, in the case of the Roseate Tern at one colony, laying has tended to coincide with neap tides, when the breeding island is most inaccessible at low tide. The only species recorded breeding both on the offshore islands and on Latham Island, the Sooty Tern, follows the same pattern as the others on the offshore Tenewe Island, laying July-August, but at Latham Island, not accessible to small canoes, it apparently lays in October, when seas are relatively calm.

On Latham Island, the Masked Booby probably lays September-November, peaking in October. The Swift Tern lays in October or November. Here, it would seem that, most breeding takes place after the end of the monsoon, when the seas become relatively calm. However, whereas inshore islands at Kiunga and other places near the Kenya-Tanzania coast have been visited outside the main breeding season (in July and August), withfinding any seabirds breeding, Island has not been visited, or if visited no records have been kept, except in October-November. There is thus no proof that seabirds do not also breed at Latham Island at other times of the year, whereas it is clear that, on the offshore islands, they breed only at the height of the monsoon when seas are rough.

Latham Island is apparently totally inaccessible by boat in the monsoon (Gerhart, pers. comm). Evidently the easiest way of ascertaining whether any breeding takes place during the time of rough seas would be aerial survey, with, if possible, photographic counts of any birds found breeding. If no breeding occurs on Latham Island during the monsoon and rough seas, then clearly the factors operating to control breeding seasons of seabirds on Latham Island and on the inshore islets off Kiunga and Lamu must be different—even, for the Sooty Tern, amongst the same species.

We have already suggested (Britton & Brown 1974) that the obvious explanation of the breeding seasons on the offshore islands of the Lamu archipelago is the rough seas prevailing in July-August, making these islands inaccessible to humans in small and primitive boats. However, it is possible also that the relatively rough seas, and the strong coastal current associated with the south-east monsoon, may result in greater upwelling of nutrientrich sea water, and a greater availability of food supplies in the shape of small fish. If this were so, one would expect seabirds to breed in greater numbers at Latham Island also during the monsoon; at present there is no evidence to indicate that they do.

Observations at other times of the year suggest that terns feeding a few kilometrés offshore have no difficulty in catching food. They apparently locate shoals of pelagic predatory fish, and the smaller fish and other marine organisms that these are feeding upon, very soon after dawn on any day. One tern first sights the fish, others immediately collect in the same areas. Terns seen flying purposefully in a certain direction frequently lead one to shoals of fish-and to other terns. Fishing seems actually easier for terns in the relatively calm waters of October-March than during August's rough seas, although thousands of terns can be found fishing during most months at certain places, such as the Malindi-Watamu banks, 10-12 km offshore. Individual fishing success has not been quantitatively assessed, but general observations do not suggest that terns would have any difficulty in catching enough food at times when they are definitely not breeding on the islands of the Lamu archipelago.

Available evidence at present leads us to believe, therefore, that climatic factors, notably the rough seas accompanying the south-east monsoon, are more important than food supplies, which appear to be perennially easy to obtain, in controlling the breeding seasons of terns, and consequently the Sooty Gull, on small offshore islands in Kenya and Tanzania. If additional data are obtained from Latham Island to indicate that the peak breeding season is October-November, when seas are calm, it will tend to confirm our present view that food supplies are relatively unimportant, but that inaccessibility of the breeding islands to small boats is critical for successful breeding among these seabirds.

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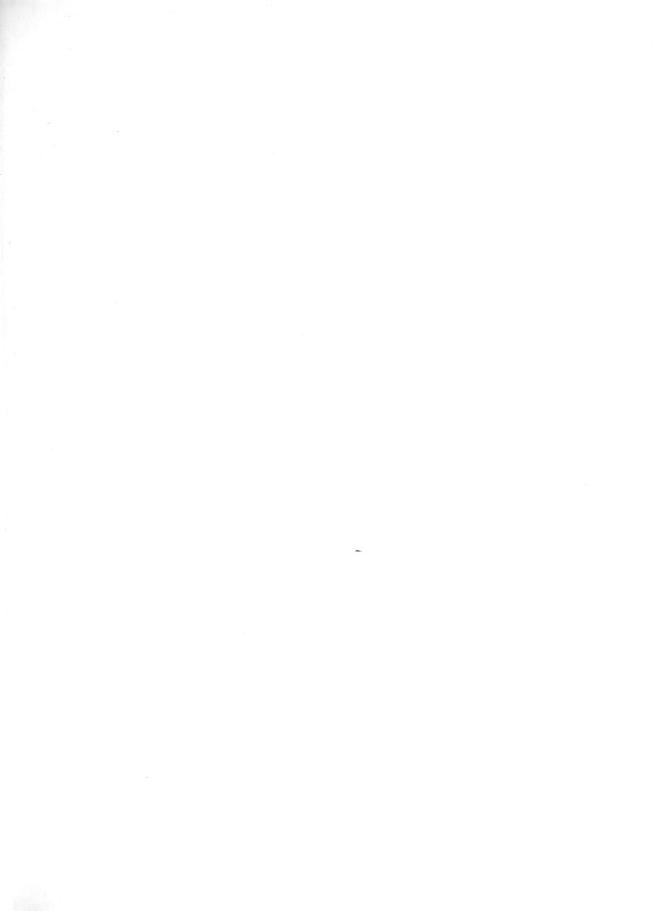
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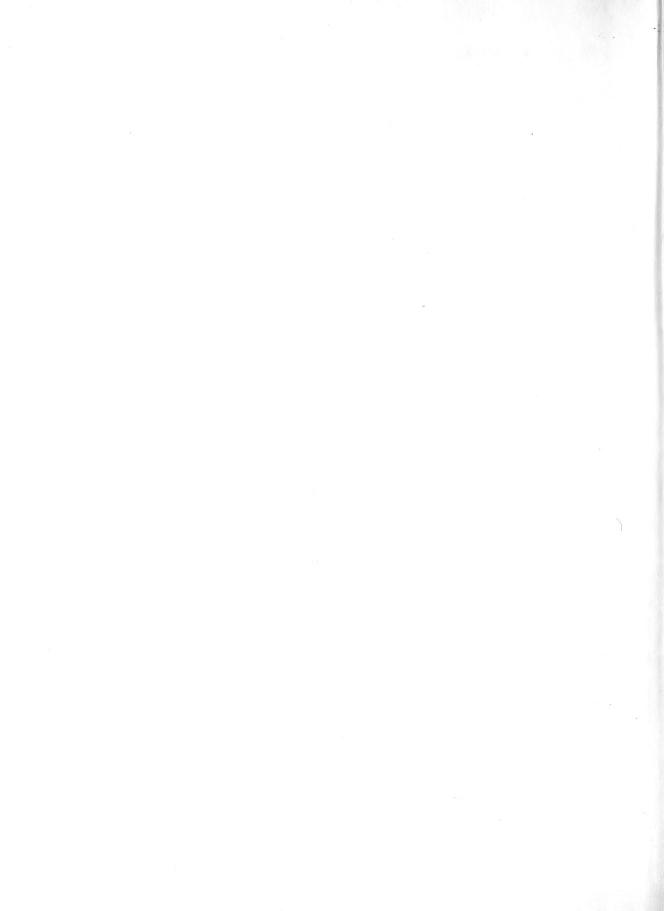
A breeding data bibliography was prepared and circulated by Mrs H. A. Britton & P.L.B. in 1972 as a prerequisite for this and other papers on the breeding biology of birds in East Africa. In addition to the foregoing, which are cited in the text of this paper, a large number of publications have been utilized in the compilation of the species accounts. Most of these are in the following English language journals from which all relevant papers have been abstracted (updated to September 1977): Annual reports of the Uganda Game & Fisheries Department, Bateleur, Bulletin of the British Ornithologists' Club, EANHS Bulletin (formerly Newsletter) Ibis, Journal of the East Africa Natural History Society and National Museum, Nature in East Africa, Oologists' Record, Ostrich, Tanganyika Notes and Records, and Uganda Journal.

Additional records have been included from the following: Bulletin of the Los Angeles County Museum of Natural History, Science 3; Bulletin of the Museum of Comparative Zoology, Harvard 89 (5); Condor 71: 140-145; Contributions in Science 84, 130, 174, 198, 211; East African Wildlife Journal 2: 164-165, 3: 130, 6: 142-144, 8: 206; Journal of Animal Ecology 7: 314-327; Journal für Ornithologie 71: 1-280; Northern Rhodesia Journal 5: 465-475; Postilla 96; Proceedings of the Zoological Society of London 1923: 899-921, 1928: 71-79, 117: 345-364; Revue Zoologique et Botanique Africaines 25 (1); 484-532; Scopus I(2): 51-52, I(3): 86-88; Smithsonian Contributions to Zoology 111; United States National Museum Bulletin 153, 223; Lynn-Allen (1951, 'Shotgun and sunlight'), Meinertzhagen (1957, 'Kenya diary 1902–1906'), van Someren (1958 'A birdwatcher in Kenya').











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